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The structure and functioning of marine ecosystems: an environmental protection and management perspective

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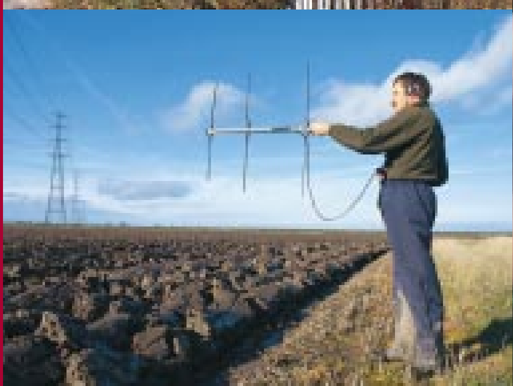

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The structure and functioning of marine ecosystems: an environmental protection and management perspective

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Colleagues at the MBA including Stuart Jenkins and Harvey Tyler-Walters have all spent time with us advising on aspects of the work.

Summary

Ensuring that the seas around the UK are '*clean, healthy, safe, productive and biologically diverse'* (Defra, 2002) whilst continuing to provide the goods and services that society uses requires:

- knowledge and understanding of what is where and how it varies with time, including physical, chemical and biological **properties**;
- knowledge and understanding of the **processes** that influence properties at a location, and
- management that understands:
    - o the role of **structural features**;
    - o the interaction of physical, chemical and biotic **processes** that shape ecosystem **functioning**, and
    - o the importance of biological diversity in the above.

Destroying or modifying the structure of habitats or biological communities, impairing ecosystem functioning and interfering with natural processes will have consequences for the 'goods and services' that the sea supplies as well as for maintaining the 'naturalness' that is widely valued on aesthetic and ethical grounds.

This report provides:

1. a summary of marine ecosystem goods and services;

2. a description of major large-scale properties and processes;

3. an account of ecosystem structure and functioning in the marine environment and examples of how environmental change from human activities may affect ecosystem structure and functioning;

4. the role of resilience, resistance and recovery in maintaining the baseline conditions;

5. examples of how the limits of ecosystem resilience and resistance may be reached, and

6. dossiers of critical ecosystem structure and functional processes within particular environments (marine landscapes).

The information listed above will support the 'Ecosystem Approach' to marine environmental management, protection and education.

The case studies given in the report are only examples but can be used to inform the importance of different aspects of properties, structure and functioning (as processes) for management of areas to maintain ecosystems and their services.

Reference

HISCOCK, K., and others. 2006. *The structure and functioning of marine ecosystems: an environmental protection and management perspective*. Report to English Nature from the Marine Biological Association. Plymouth: Marine Biological Association. English Nature Contract MAR08-02-015.

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1 Introduction

Ensuring that the seas around the UK are '*clean, healthy, safe, productive and biologically diverse*' (Defra, 2002) whilst continuing to provide the goods and services that society uses requires:

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Destroying or modifying the structure of habitats or biological communities, impairing ecosystem functioning and interfering with natural processes will have consequences for the 'goods and services' that the sea supplies as well as for maintaining the 'naturalness' that is widely valued on aesthetic and ethical grounds.

In assessing the role of ecosystem structure and functioning, it is also important to identify where resistance, resilience and recovery overcome potentially adverse human impacts and to give examples of where human activities do matter because natural processes will not overcome the effects of those activities.

This report provides:

1. a summary of marine ecosystem goods and services;

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The information listed above will support the 'Ecosystem Approach' (see Boxes 1 and 2) to marine environmental management, protection and education.

The case studies given in the report are only examples but can be used to inform the importance of different aspects of properties, structure and functioning (as processes) for management of areas to maintain ecosystems and their services.

A glossary is also available at the end of the report in case some words used in the text are unfamiliar.

Box 1. Definitions of the Ecosystem Approach

"*The ecosystem approach is a strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way. The application of the ecosystem approach will help to reach a balance of the three objectives of the Convention: conservation; sustainable use; and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources*."

Convention on Biological Diversity, 2000

"*The ecosystem approach is the comprehensive integrated management of human activities, based on best available scientific knowledge about the ecosystem and its dynamics, in order to identify and take action on influences which are critical to the health of the marine ecosystems, thereby achieving sustainable use of ecosystem goods and services and maintenance of ecosystem integrity*."
EU Marine Strategy Stakeholder Workshop, Denmark, 4 – 6 December 2002

Box 2. Some of the 12 principles recommended by the Conference of Parties of the Convention on Biological Diversity in 2000 to guide signatory countries in the practical application of the ecosystem-based approach (items referring to structure and functioning are highlighted.)

- The ecosystem approach should be undertaken at the appropriate spatial and temporal scales.
- Recognising the varying temporal scales and lag-effects that characterise ecosystem process, objectives for ecosystem management should be set for the long-term.
- Ecosystem managers should consider the effects (actual or potential) of their activities on adjacent and other ecosystems.
- Conservation of ecosystem structure and functioning, in order to maintain ecosystem services, should be a priority target of the ecosystem approach.
- Ecosystems must be managed within the limits of their functioning.

The ecosystem approach should seek the appropriate balance between, and integration of, conservation and use of biological diversity. See www.biodiv.org

In this report, we adopt the definition of **ecosystem functioning** from Naeem and others (2004):
"the activities, processes or properties of ecosystems that are influenced by its biota".

2 Marine 'ecosystems'

An 'ecosystem' is the combination of organisms with their physical environment interacting as an ecological unit (from Lincoln and others1998). The ecosystem is a deep rooted concept in ecology stemming from the pioneering work of scientists such as the Odums and Likens. An ecosystem can be as large as the North Sea to as small as the bacteria and their environment in the gut of a fish (Figure 1). For fisheries conservation, it will most likely be necessary to assess ecosystems at the large (North Sea) scale while, for nature conservation and assessing the likely impacts of human activities, consideration is more likely to be at the scale of physiographic (landscape) features such as an estuary or an offshore reef.

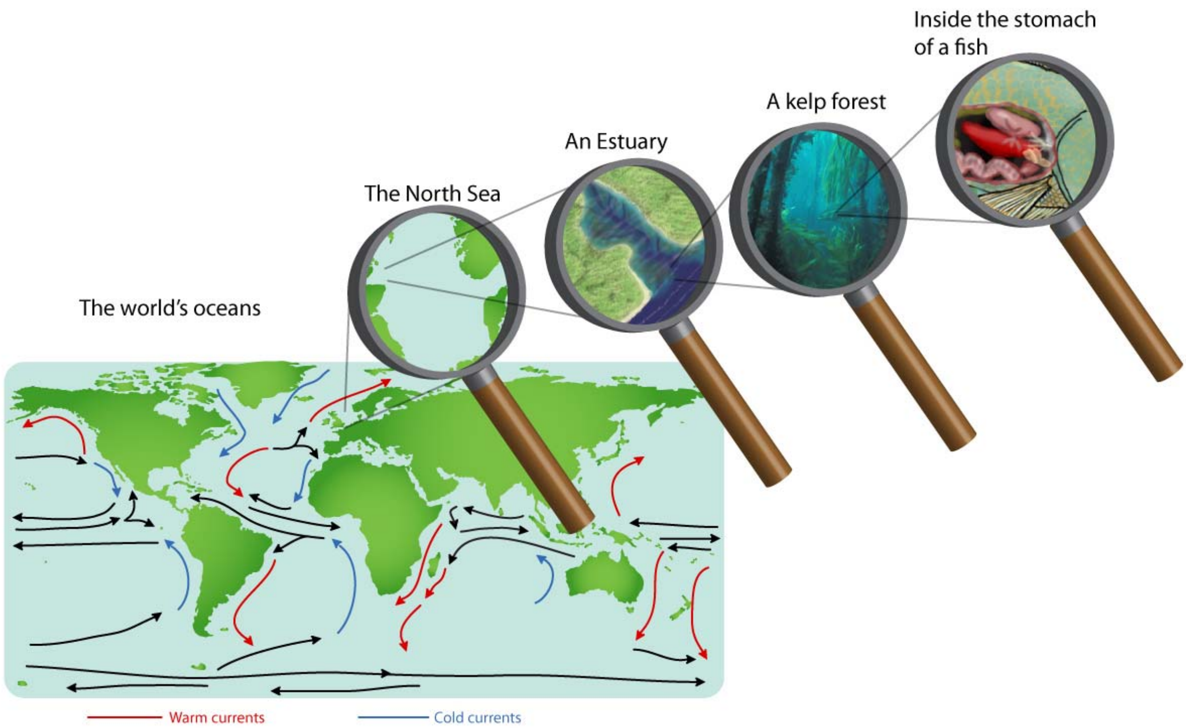


Figure 1 An 'ecosystem' can be as large as the North Sea to as small as the bacteria and their environment in the gut of a fish. Drawing: Jack Sewell.

Marine ecosystems are different from terrestrial ecosystems in a number of ways including greater propagule and material exchange and more rapid biological processes (Giller and others 2004). These properties and processes are due the fluid nature of marine ecosystems which make them dynamic, often unpredictable and, ultimately, highly complex systems. As a result of this fluidity, the boundaries of marine ecosystems are often difficult to identify. Propagules, where they are long-lived, are readily dispersed and movements of planktonic and fish species are generally unimpeded by barriers, thus many marine ecosystems are considered more open than terrestrial systems such as grasslands or freshwater ecosystems such as ponds and lakes.

In the following chapters we describe how properties, structure and processes affect the functioning of an ecosystem and hence its human value via goods and services provided. It should be stressed that these elements are by no means independent and act together to influence the functioning of marine ecosystems. Figure 2 illustrates some of the properties and processes associated with a kelp holdfast community.

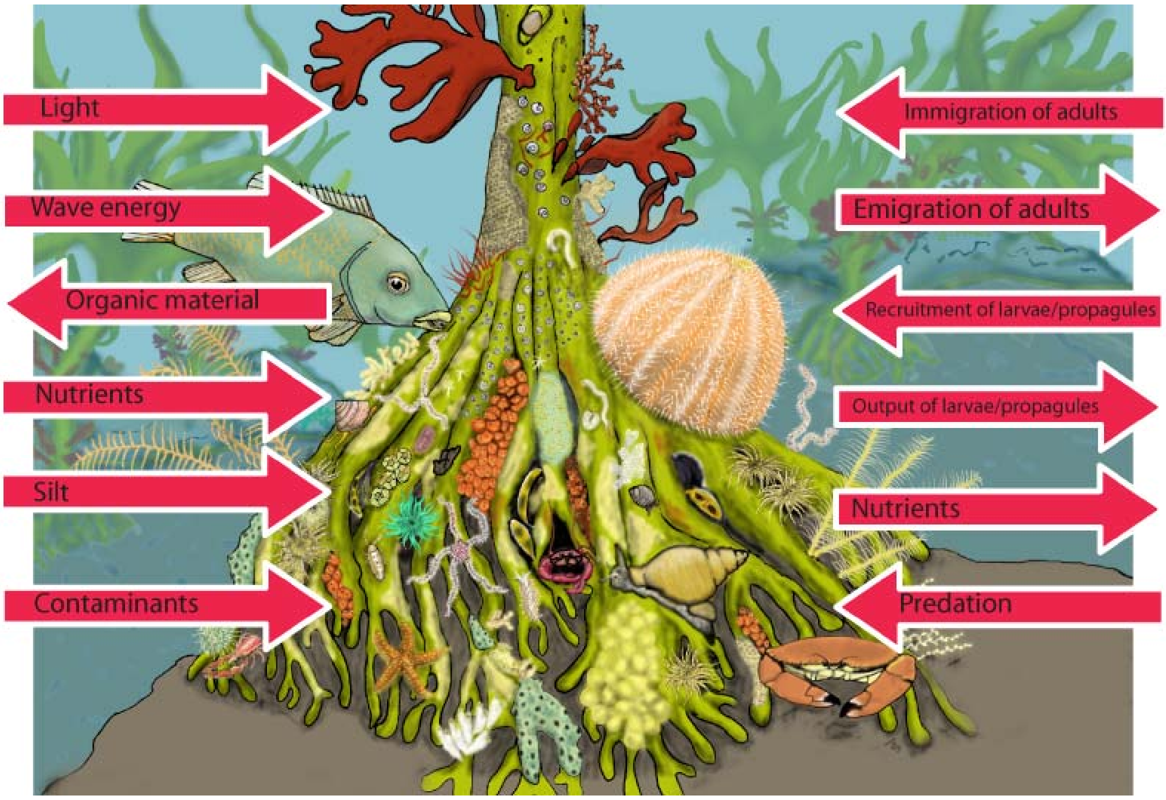


Figure 2 A community of species associated with a structural feature: a kelp holdfast. The main inputs and outputs (arrows) in terms of properties and processes are shown. Drawing: Jack Sewell.

3 'Goods and services' provided by marine biodiversity

The microbes, plants and animals in marine ecosystems provide numerous goods and services for society. Some of those goods and services, as illustrated in Figure 3, are obvious and it is easy to understand how humans benefit from them. These goods and services are often referred to as "direct". Direct goods and services are usually easier to identify because there is an obvious link with financial profit. Other goods and services are equally vital although the way in which we benefit from them is less apparent. As such, it has historically been difficult to put a price on them. These "indirect" goods and services include bioremediation of waste and nutrient cycling.

The marine environment provides additional services regardless of biodiversity, for example, transport. The total value of the world ecosystem's goods and services to humans has been estimated to be $33 trillion per annum with approximately 63% of the contributed by marine systems (worth US$20.9 trillion per year (Costanza and others 1997). Beaumont (2003) gives estimates of the value of goods and services provided by UK marine biodiversity. Examples are:

1. Annual non-use value of sea mammals: £474 -1,149 million.

2. Value of landings sea fishing industry: £546.3 million, stimulating around £800 – 1,200 million per year of economic activity.

3. Putting nitrates and phosphates back into food chains: £0.10 – 0.28 per m^3.

4. Absorbing and trapping excess carbon dioxide and slowing climate change: £16 – 164 per tonne of carbon stored.

5. Purifying effects of wetlands: £1097 – 1237 per acre.

6. Disturbance prevention by wetlands (flood and storm protection): £2,616 million.

7. Recreation and tourism (contributes to): £17,000 million p.a.

8. Recreational angling: £1,000 million p.a.

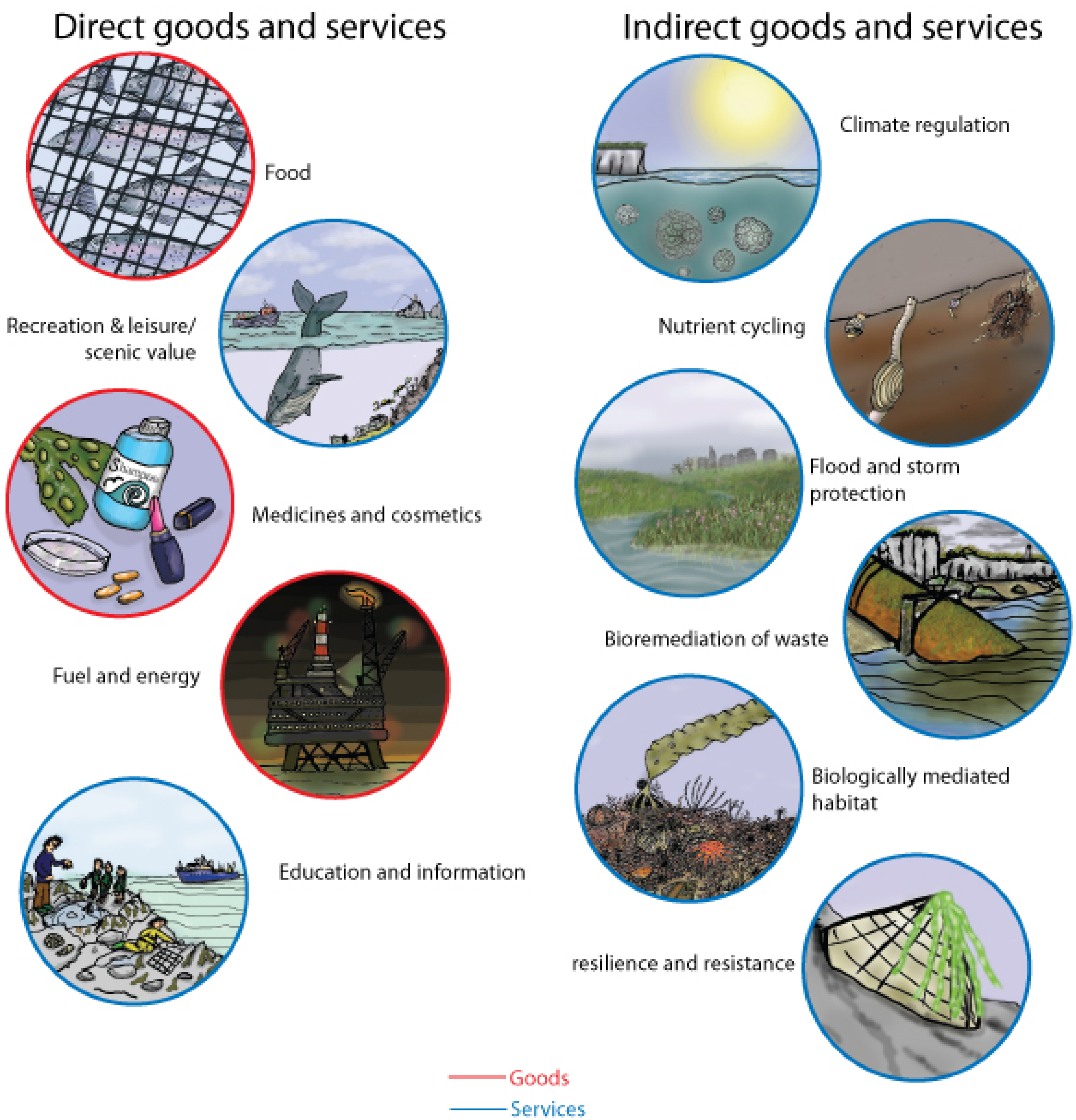


Figure 3 Goods and services provided by marine biodiversity. Adapted from Beaumont and others (2006) and other sources and corresponding to the marine goods and services in the Millennium Ecosystem Assessment (2005). Although a 'biologically mediated habitat' and 'resilience and resistance' can be seen as properties of an ecosystem, they are essential for the provision of some goods and services. Drawings: Jack Sewell.

The continued (sustainable) supply of those goods and services often relies on the presence of and interaction between marine organisms. Whilst the goods and services that the sea provides for humans are reasonably easy to catalogue and understand, the way in which the living resources in the sea interact and rely on each other and the environment around them is less easy to identify. However, understanding those interactions is essential if we are to use the seas sustainably and prevent irreversible damage as a result of human activity. To understand how ecosystems 'work' we will consider the 'properties and large scale processes' of marine ecosystems, how ecosystems are 'structured' and the processes that shape their functioning.

4 Properties and large scale processes

The functioning of an ecosystem is affected by its properties and the processes occurring within it, including those influenced by its biota (biodiversity). Properties can affect processes and *vice versa*. For example, the turbidity (a property) within an estuary will affect the level of primary production (a process) with lower turbidity leading to enhanced primary productivity. Conversely, bioturbation (a process) can increase small-scale turbidity at the sediment-water interface in silty areas.

In this section we discuss the properties and processes that are the broad-scale features of marine ecosystems and which influence large scale biological properties such as biogeographical distribution. We also discuss more localised aspects of structure and functioning including biologically mediated properties and processes that are part of the functioning.

4.1 Properties

The physical, chemical and biological properties of the seas around the UK are described in Hiscock (1996). The predominant physical and chemical properties defined at a large scale are:

- Temperature range (air and sea for intertidal areas, seawater for subtidal areas);
- Salinity including maxima and minima;
- Substratum type;
- Light regime;
- Turbidity;
- Residual current strength and direction;
- Strength of wave action;
- Strength of tidal streams;
- Stratification of the water column;
- Nutrient status, and
- Contaminant levels.

Biological properties include assemblage (biotope) composition and trophic structure. At a community level, properties can include resilience and resistance (Giller and others 2004) which are themselves influenced by the trophic structure and composition of those communities.

4.2 Processes

'Processes' exert a dynamic influence on the marine environment that 'drive' what is present where and how it changes. They can be physical, chemical and biological. Figure 4 highlights some of the process that control shallow marine communities in the North east Atlantic.

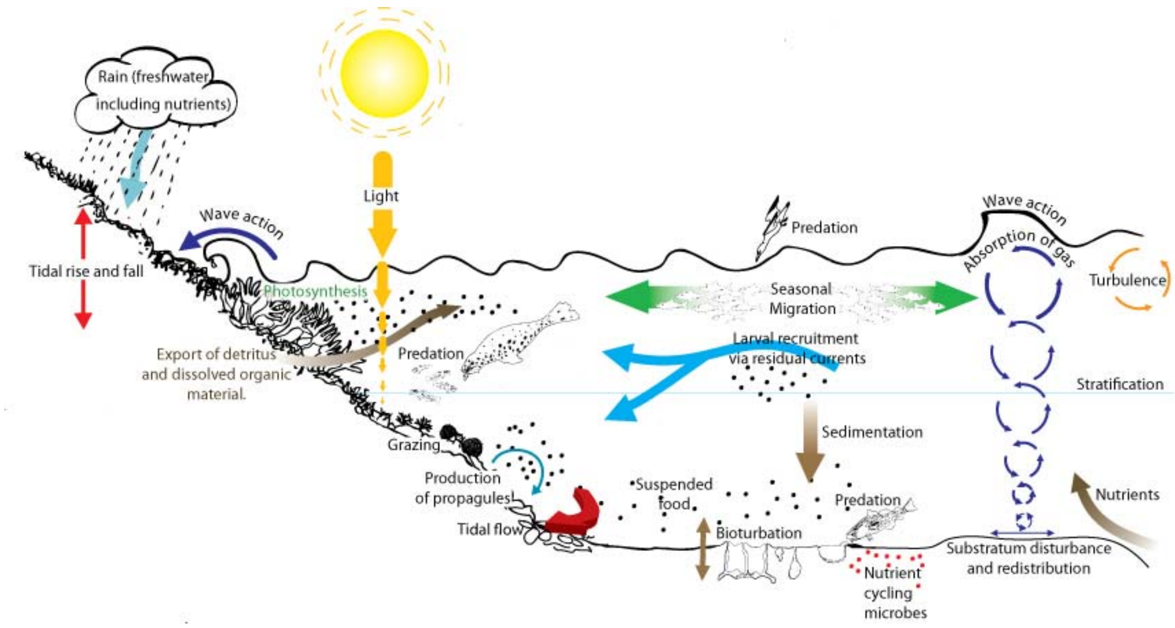


Figure 4 Physical, chemical and biological processes that influence shallow marine communities in the NE Atlantic. Drawing: Keith Hiscock & Jack Sewell.

Processes can act together to influence the properties and structural elements of marine ecosystems. For example, physical properties such as tidal flow and processes such as sedimentation can greatly influence the sediment characteristics and presence / absence of certain species at a given location. Strong tidal currents favour coarse sediment such as gravel and pebbles while slow currents favour muddy sediment.

Other processes which often are or have physical, chemical and biological elements include:

- Dispersal of water quality characteristics brought about by movement of water masses;
- Gas exchange;
- Nutrient exchange;
- Primary and secondary production;
- Bioturbation;
- Reef-building, and
- Propagule dispersal brought about by movement of water masses.

Figure 5 highlights the importance of water movement for the large-scale distribution of water masses and larvae which has implications for the recovery of communities and habitats following disturbance, and for the extension of species distributions.

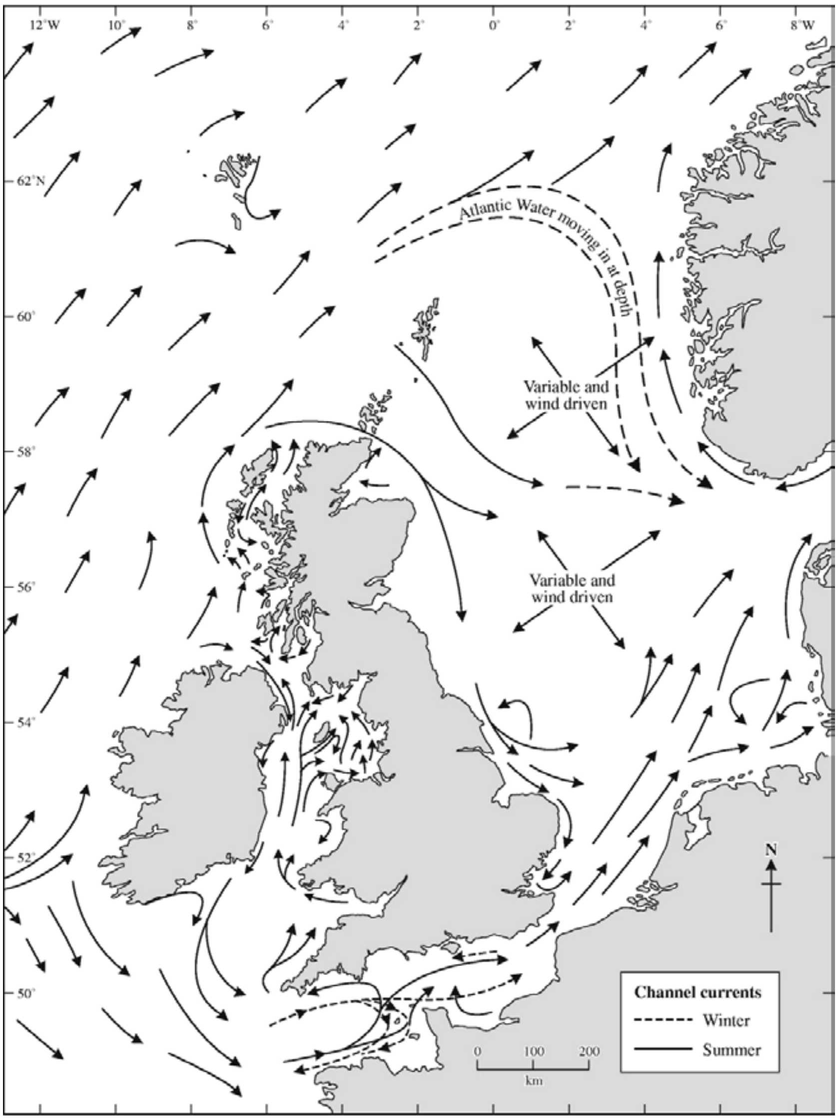


Figure 5 The direction of residual currents around the British Isles is important for the distribution of water masses and of larvae. From: Hiscock (1998), re-drawn from Lee and Ramster (1981).

Primary production. Primary production is the basis of all living processes. The most visible primary producers are the macroalgae and angiosperms (sea grasses) that live attached to the seabed (Plate 1). But the highest levels of primary production come from minute planktonic organisms (Plate 2). Primary producers assimilate carbon through photosynthesis and take-up nutrients (nitrogen, phosphorous and other minerals) to create biomass. In turn, plants are consumed by animals or the carbon is made available in other ways such as by death, fragmentation and decomposition to create the detritus (seston) that suspension feeders may use.

Primary productivity is often restricted by limited nutrient availability. However, where nutrients are enhanced, for instance from agricultural run-off or sewage disposal, green algae may become extensive on the shore and phytoplankton blooms may occur.

Plate 1 Laminaria dominated communities have annual productivity rates of approximately 2 kg carbon m^{-2} y^{-1} compared to temperate grasslands, which are generally less than 1 kg carbon m^{-2} y^{-1} (see Mann, 1972a,b; Mann & Chapman, 1975; Kaiser and others 2005). Image: Keith Hiscock.

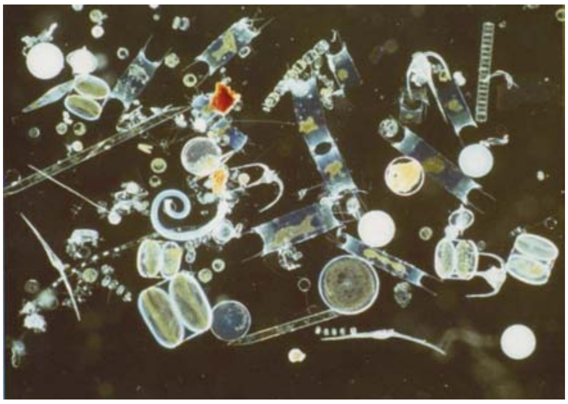


Plate 2 Coastal phytoplankton annual production is generally less than 1 kg carbon m^{-2} y^{-1} (see Woodwell and others 1973; Kaiser and others 2005) but total input to the inshore marine environment is much larger because of the extent of the seas. Image: Norman Nicoll / www.naturalvisions.co.uk

5 Structure

The term 'structure' is commonly understood to mean: "**the arrangement of and relations between the parts of something complex**" (Pearsall, 1999). In ecology, the 'structure' of an ecosystem is usually defined to include amounts and nature of both biological and non-biological components of the ecosystem as described above (see Odum, 1962; Mathews and others 1982).

5.1 Non-biological structure

The physical structure of substratum or the physical and chemical structure of the water column is highly influential in determining the sort of marine life that is likely to be present at a location. For the seabed, the categories of structure recorded in Marine Nature Conservation Review (MNCR) surveys were:

Features – Rock

Surface relief	overall relief of the habitat from **very even** (unbroken bedrock with uniform inclination) to **very rugged** (highly broken slope with wide range of surfaces, possibly with gullies or rockpools breaking up the overall inclination considerably).
Texture	an indication of the smoothness of the rock type from **very smooth** (a hard and well worn rock such as granite or well rounded cobbles) to **highly pitted** (a highly pitted or bored rock such as some limestone, or very fragmentary and jagged rock such as shale).
Stability	an indication of the stability of the rock, and related to wave action, from **very stable** (bedrock; boulders which are never moved by wave action) to **highly mobile** (frequently turned pebbles, cobble or even boulders, where colonisation is considerably affected because of such movement).
Scour	an indication of scour by sand (not abrasion from mobility of rocks - see above), from **none** (no scour present) to **highly scoured** (very highly scoured by sand - rocks likely to be smooth and without colonisation).
Silt	the amount of silt settled on the rocks, from **none** (very clean rock surfaces) to **highly silted** (thick layer of silt on all surfaces). Where sand deposits on rocks from wave action note under the tick-boxes of this section.
Fissures	the amount of fissures (over 10 mm wide) present, from **none** to **very many** (accounts for high proportion of habitat).
Crevices	the amount of crevices (less than 10 mm wide) present, from **none** to **very many** (accounts for high proportion of habitat).
Rockpools	the amount of rockpool present, from **none** to **very many** (accounts for high proportion of habitat).
Boulder, cobble, pebble shape	from **highly rounded** (very rounded boulders, cobbles or pebbles) to **very angular** (highly angular boulders, cobbles or pebbles, eg slates).

Additionally to the information required by MNCR surveys, the softness and hardness of rocks is important. For instance, rich algal communities may occur if the rock retains water or is soft enough to allow penetration of holdfasts. Rocks which are soft enough to allow animals to bore into them provide security from predators and, when the inhabitant dies, a habitat for nestling species.

Features – Sediment

Surface relief	overall relief of the habitat, from **very even** (surface completely uniform) to **highly uneven** (surface perhaps with numerous mounds or drainage channels).
Firmness	an indication of the degree of softness or compactness of the sediment, on the scale (with littoral and sublittoral guides): 1 **very firm** (no indentation when walked on; difficult to dig with fingers), 2 (make a slight indentation; fingers only in), 3 (sink ankle deep; hand in), 4 (sink knee deep; can penetrate up to elbow) to 5 **very soft** (sink thigh deep; whole arm in).
Stability	from **highly stable** (movement of sediment very unlikely) to **highly mobile** (sediment constantly being moved).
Sorting	[particle-size distribution] - an indication of the uniformity of the particle size, from **very well sorted** (sediment composed of a single grain size) to **very poorly sorted** (sediment with wide range of grain sizes).
Black layer	an indication of the depth of the anoxic layer, on the scale: 1= not visible, 2 >20 cm below surface, 3=5-20 cm below surface, 4=1-5 cm below surface, 5=<1 cm below surface.

(From Hiscock, 1996)

The physical environment ‘habitat’ with its distinctive assemblage of species biological 'community' is often referred to as a biotope. Biotopes are classified according to the physical and chemical structure of habitat and also by the species found within them (see Figure 6).

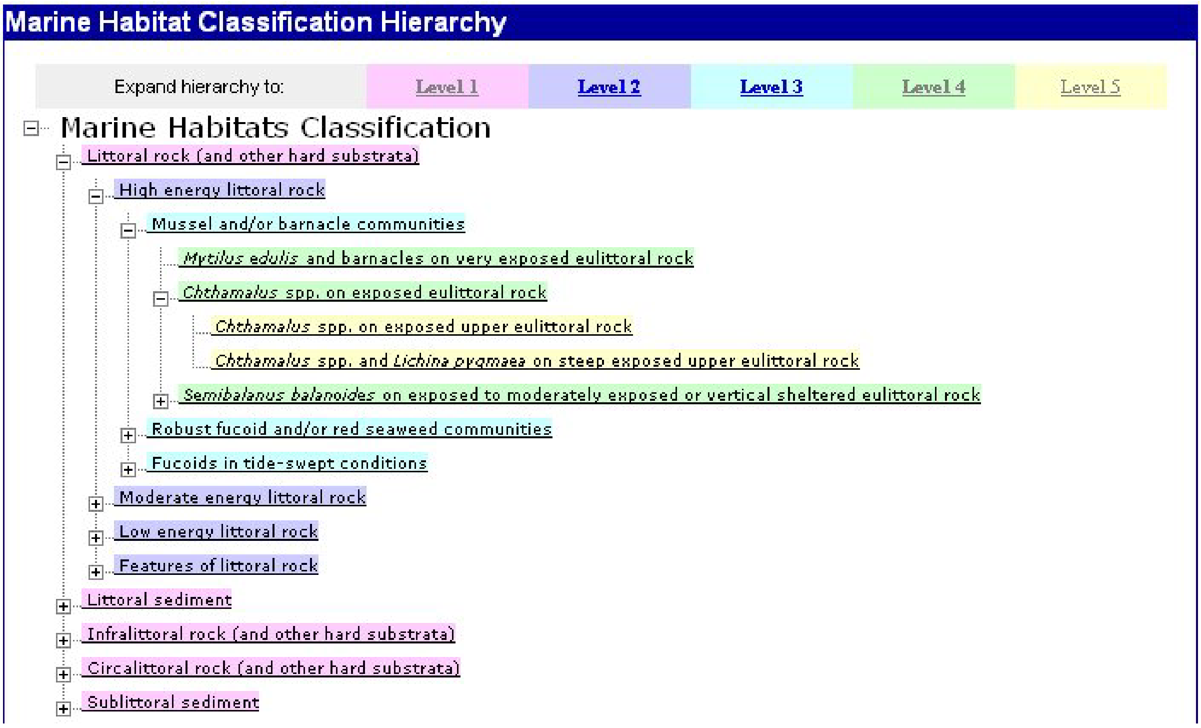


Figure 6 A part of the biotopes classification hierarchy (from: http://www.jncc.gov.uk). The classification identifies the major physical and chemical features that characterise the habitat component and the species that colonise it and make-up the biological component of the biotope. Only one part of the selection has been expanded in this figure.

5.2 Biological structure

By referring to biological structure in this context, we mean it to include both the actual physical structure provided by animals and plants (eg biogenic structures) and the structural organisation of the community itself – the composition and relative proportions of species present at a locality. Plants and animals create physical structures that are, in some cases, essential for maintaining species richness and influencing ecosystem processes. Some of those structures are biogenic reefs that may be an 'oasis' of species richness in often apparently barren or impoverished settings (see Figure 7 and Plate 3).

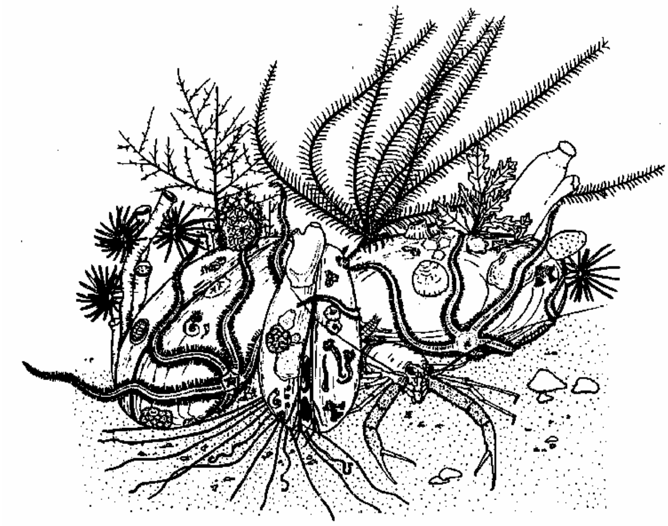


Figure 7 Biogenic reef structures such as those formed by horse mussels *Modiolus modiolus* increase habitat complexity and provide a home for a wide range of species. Drawing: Sue Scott.

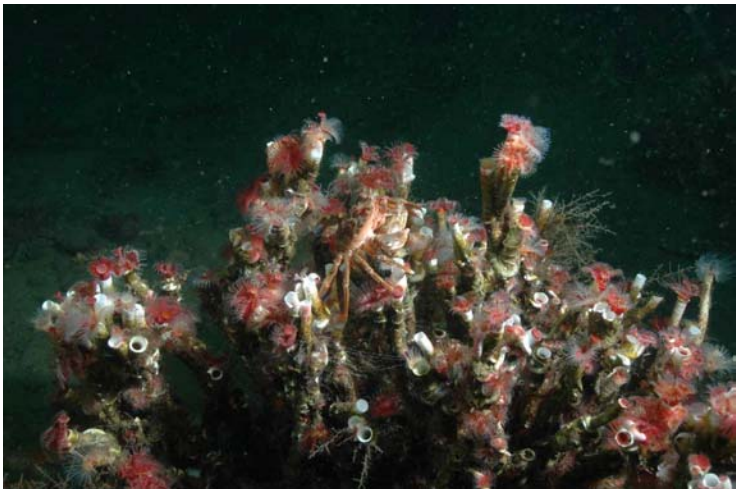


Plate 3 The reef-building tube worm *Serpula vermicularis* is a key structural species that, if destroyed, the associated community is lost. Image: Keith Hiscock.

Plants and animals may also provide micro-habitats for refuge from predation, including grazing, or protection from adverse conditions such as strong tidal currents. Often, they are nursery areas for juvenile fish or shellfish. Often, they are easily destroyed or damaged by human activities.

Species that themselves create structure because of their physical presence or their activities, especially burrowing, are described as **'Key structural species'** or **'ecosystem engineers'.** The sorts of important structures that they create include:

- hard substratum for attachment of sessile species;
- surfaces suitable for laying eggs on / in, and
- burrows that provide a refuge for other species (Figures 8 & 9).

Figure 8 Some species are capable of boring into soft rock such as chalk and limestone, creating a structure of holes and galleries where they are protected from predators. When they die, those holes become available for cryptic species to use. Section of limestone rock from Firestone Bay, Plymouth. Drawing: Sue Scott.

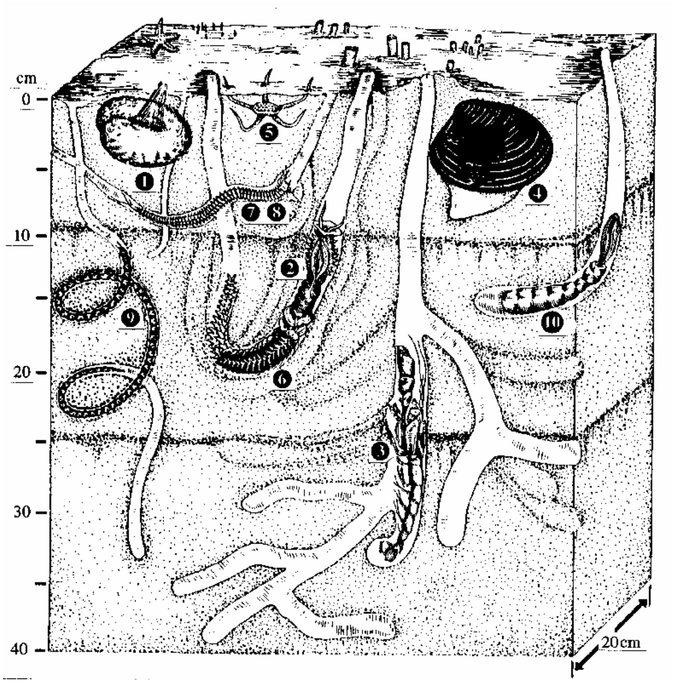


Figure 9 Sediments may appear barren on the surface or occupied by a few crawling species but the majority of species are hidden and many create burrows and galleries that structure and re-structure the sediment enabling its irrigation. The community present on the Oyster Ground, Belgium. From: de Wilde and others (1984). 1. Spatangoids (includes *Echinocardium cordatum*, *Echinocardium flavescens*, *Brissopsis lyrifera*). 2. *Chaetopterus variopedatus*. 3. Callianassids (includes *Callianassa subterranea*, *Upogebia deltaura*). 4. *Arctica islandica*. 5. Ophiuroids (includes *Amphiura filiformis*, *Amphiura chiajei*). 6. *Gattyana cirrosa*. 7. *Glycera rouxi*, *Glycera alba*. 8. Nereis (now *Hediste*) and *Nephtys* spp. 9. *Notomastus latericeus*. 10. *Echiurus echiurus*.

These key species may also change aspects of the physical and chemical environment by, for instance, trapping silt or by facilitating oxygenation of sediments. Key structural species and ecosystem engineers are usually dominant species in an assemblage.
As with processes, structure can operate on many scales. Small-scale structure might include the habitat offered by an empty burrow. At a larger scale, structure might refer to the organisation of the community as a whole, in terms of trophic levels, species richness and functional diversity. These attributes can also be viewed as properties.

5.3 Structural vulnerability

Architectural structure whether of burrows in sediments, biogenic reefs or the shelter afforded by seagrass beds or kelp forests, is highly vulnerable to physical disturbance. For instance, Strangford Lough, Ireland, was the site of extensive horse mussel (*Modiolus modiolus*) beds. These beds were structurally complex and, as a result, extremely species rich. However, as a result of scallop dredging these beds have been flattened and the associated community destroyed (eg Magorrian & Service, 1998; Roberts and others 2004). Rich examples of horse mussel beds in the North basin, described in the 1990s were found to be 'very much reduced in extent' in 2003 and the beds in the central channel showed a 'significant decline', with a decrease in *Modiolus* in transects from 45% in 1989 to <2% in 2003 (Roberts and others 2004). Densities per square metre also show 'significant declines' between the mid 1970s and 2003 (Roberts and others 2004).

Community structure includes the balance between the relative abundance of different species. For key functional species, a change in the balance can lead to major changes in the dynamics of the community which in turn can affect the functioning of the system (see for example section 6.1.1).

Alien species may also threaten structural integrity. For instance, the slipper limpet *Crepidula fornicata* changes the substratum where it is dominant (Figure 10). That change can be from coarse sediments to shell and pseudofaeces characterised sediments creating an entirely different biotope.

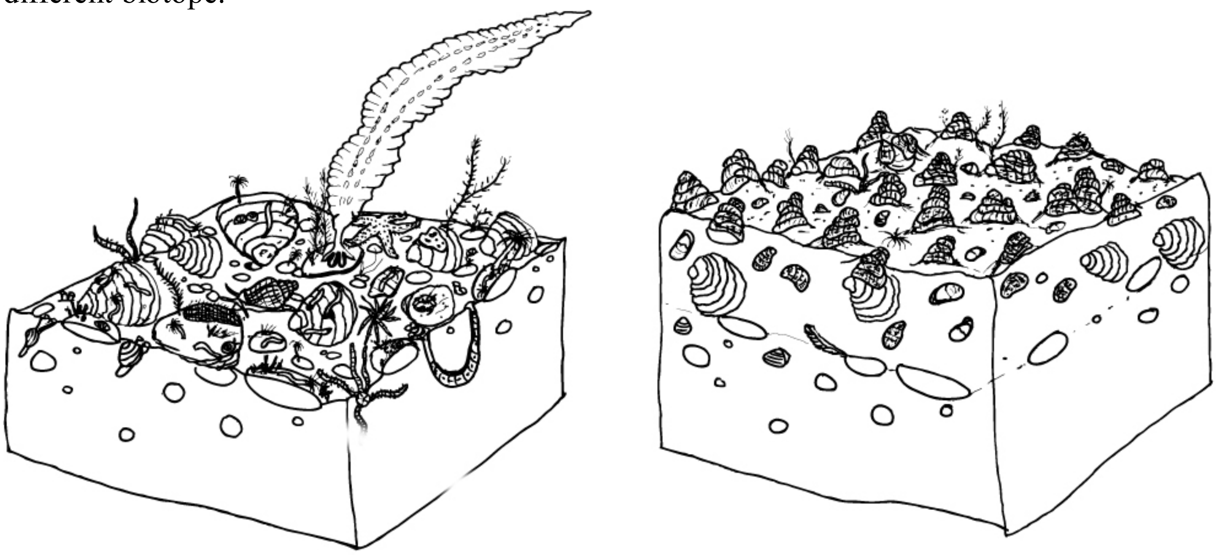


Figure 10 (a) Seabed dominated by the native oyster *Ostrea edulis*. (b) Seabed, previously dominated by the native oyster *Ostrea edulis*, now dominated by the invasive slipper limpet, *Crepidula fornicata*. Images: Jack Sewell.

Plate 4 illustrates an intertidal area previously dominated by edible mussels. Since the area was invaded by the Pacific oyster, the structural properties of the habitat are now different.

Plate 4 In the Netherlands, the invasive Pacific oyster *Crassostrea gigas* has displaced previously harvested mussels *Mytilus edulis.* Due to the fact that the oysters are concreted together, they cannot be harvested, although in terms of ecosystem structure, the oysters probably fulfil the same role as mussels. Image: Norbert Dankers.

6 Ecosystem functioning and biodiversity

Box 3. Biodiversity – an integral part of ecosystem function (based on Smith and others 2006):
"Biodiversity is an integral part of ecosystem function, affecting ecosystem productivity, decomposition rates, nutrient cycling, stability, and resistance to perturbations. Declines in biodiversity are of great concern as forces such as habitat destruction, global environmental change, pollution, and exotic species cause continued extinctions and declines in species abundances and community biodiversity. …… An integral part of understanding the crisis of biodiversity loss is continued investigations and documentation of long-term community change."

Attributes of coastal and nearshore ecosystems that are important to the functioning of those systems include:

- the oceanographic and coastline setting including currents, upwelling, waves and coastline complexity;
- the fact that they are largely 'open' and therefore the import and export of material (detritus, plankton) is facilitated;
- there are sharp physical gradients (especially on shores and in estuaries) including depth, tidal elevation, wave action and salinity;
- little primary production is consumed at the place of origin;
- fluctuations will be driven by variability in recruitment;
- there are strong biological interactions with a few species or functional groups having disproportionate effects.

The elements of ecosystem functioning that are influenced by biota include:

- energy transfer;
- elemental cycling (carbon, silicon, nitrogen, phosphorus, sulphur, calcium);
- productivity;
- food supply / export, and
- modification of physical processes.

6.1 The role of species: biological traits

Ecosystem functioning is mediated through the activities of species that make-up the biodiversity in an area. For instance, ecosystem functioning may greatly depend on the proportions of producers and consumers and the presence of grazing species. By looking at certain characteristics that govern the lifestyles of species, it may be possible to indicate how those species influence ecosystem structure and functioning. Such features include size, mobility, feeding methods, reproductive strategy and dispersal potential. Such characteristics are often referred to as 'traits'. Biological traits can be assigned to any aspect of the life of the species including reproduction, habitat preferences and general biology (see Box 4). Reproductive traits include fecundity (number of eggs / young) and developmental mechanisms and it is often possible to make inferences about one from the other. For example, an animal that broods its offspring will most likely produce far fewer offspring than an animal producing planktotrophic (feeding on plankton) larvae.

Box 4. 'Biological Traits' that distinguish one species or group of species from another. *MarLIN* key information reviews for marine species contain the following traits information:	
General Biology	Body size Mobility eg *sessile / swimmer / crawler / burrower* Environmental position eg *infaunal / pelagic / epibenthic* Feeding method eg *predator / suspension feeder / deposit feeder / parasite*
Range and distribution / habitat preferences	Resident / migratory eg *resident / diel / seasonal feeding* Substratum preferences eg *maerl, cobbles, muddy sand* Tidal strength preferences eg *weak (negligible) / strong (3-6 kn)*
Reproduction and Longevity	Reproductive type eg *fission / permanent hermaphrodite* Fecundity eg *1 / 1,000-10,000 / 1,000,000* Dispersal potential eg *<10m / 10-100m / >1000m*

Traits can be scored according to the extent to which the species express them and these scores can then be weighted by abundance / biomass and summed to provide a measure of the prevalence of each functional trait over an entire assemblage (see Bremner and others 2006). Traits can also be used to make some assumptions about how the animal might respond to disturbances. With regard to the environmental position and mobility traits of a species for example, a permanently attached species growing on the seabed (such as a sea fan) is much more likely to be damaged by beam trawling than a burrowing animal that lives deep down in the sediment.

Species with similar traits often have similar habitat preferences and so it is possible to derive information about the functional requirements of groups of animals and algal species. This is of importance when determining the habitat requirements of species that underpin essential processes and functions within systems.

Certain traits will be of critical importance to the maintenance of ecosystem functioning. Critical processes include oxygenation, nutrient cycling and gas exchange. For instance, the process of bioturbation has been reported as being essential for nutrient cycling, oxygenation of the sediment and maintaining biodiversity in many sedimentary communities. Deposit feeding and burrowing traits can be used as indicators of organic matter decomposition since both activities result in bioturbation which increases oxygen and detritus penetration into the sediment (Bremner and others 2006). Suspension feeding species may be important in reducing turbidity and therefore improving light penetration for photosynthetic species (eg Cloern, 1982).

Species that provide critical services or greatly influence the type of community that develops at a location and whether or not other species will occur may be described as **key functional** species. Key functional species include grazers and predators. The edible sea urchin and wolf fish are two such species (Plates 5 and 6).

Plate 5 The sea urchin *Echinus esculentus* is a key functional species that is of critical importance in providing space for new settlement. See Jones & Kain, 1967. Image: Keith Hiscock.

Plate 6 The wolf fish *Anarhichas lupus* is a key functional species that eats sea urchins and may therefore influence the extent to which space is cleared. Image: Fiona Crouch.

'Functional diversity' occurs in communities with species that fulfil several different functional roles in the community. A community may include many passive suspension feeders, a few grazers and a few predators. Loss of one of those suspension feeders may cause little difference to the overall functioning of the community including food supply for predators ('functional redundancy') but loss of one previously abundant predator may make a great difference if there is no other species that can replace it in terms of function.

Recently, there has been growing concern about how loss of biodiversity might affect ecosystem functioning. In sediment communities it is often key functional species that dominate and bioturbation is especially important. Aside from the structure that can be provided by the burrowing and feeding habit of various infauna, functional influences of bioturbation include increasing oxygen penetration into the sediment, enhancement of nutrient cycling, and increased biodiversity.

Osinga and others (1995) looked at the effects of the sea potato *Echinocardium cordatum* (a burrowing deposit feeder) on organic-enriched benthic boxcosms. They found that the activity of the sea potato led to enhanced transport of oxygen into the sediment, which resulted in a reduction in the accumulation of toxic sulphide compounds in the sediments.

Widdicombe and others (2004) investigated the potential knock-on effects of losing bioturbating species that may be vulnerable to fishing disturbance. The heart urchin (*Brissopsis lyrifera*), sea mouse (*Aphrodite aculeata*) and brittlestar *Amphiura chiajei* are all potentially sensitive to fisheries disturbance but their importance is demonstrated by results from the mesocosm experiments that demonstrated a positive linear relationship between their abundance and species richness. The sea mouse and heart urchin are both said to 'bulldoze' through the sediment in search of food. As a result, their activities may promote diversity through increased oxygenation and sediment mixing which may enhance the cycling of nutrients between the benthos and the overlying water column and also ameliorate the impacts of eutrophication (Widdicombe and others 2004). This cycling of nutrients, termed 'bentho-pelagic coupling' is achieved through the activities of microbes, bioturbators, macrofauna and fish (Weslawski and others 2004). Another species, *Nereis diversicolor*, through the irrigation of its burrows, significantly increases the total surface area over which sediment-water exchange can take place (Davey & Watson, 1995). As a result, these authors reported that *Nereis diversicolor* in the Tamar estuary could account for fluxes to the water column of an order of magnitude more soluble ammonium than is derived from riverine and sewage sources.

Costanza and others (1997) calculated that the average global value of nutrient cycling services provided by estuaries and seagrass / algal beds are in the region of US $21,000 and US $19,000 per hectare per year respectively.

Unfortunately neither the presence of bioturbating species nor the benefits associated with their activities are conspicuous in the same way that, for example, the loss of a biogenic reef may be. Thus, their sensitivity to disturbance is all too often ignored in terms of fisheries management.

6.1.1 Structure and functioning relationships: kelp forests

The following example aims to elucidate the importance of structure provided by plants and animals in terms of ecosystem functioning. The example highlights the delicate balance between alternate states and how shifts can result in large changes to the functioning of the system; in this case, from an ecosystem characterised by the production of organic material and export of biomass to an ecosystem dominated by consumers.

Kelp forests are some of the most productive habitats in all the oceans. Kelps are major primary producers; up to 90% of kelp production enters the detrital food web and kelp is probably a major contributor of organic carbon to surrounding communities (Birkett and others 1998). Kelp beds are also species rich habitats and over 1,800 species have been recorded in the UK kelp biotopes (Birkett and others 1998).

Kelp forests are a good example of a habitat where structural species dominate. The kelps themselves are the physical habitat that provides, amongst much else, shelter for fish, food for herbivores and an attachment sites for the eggs of invertebrates. Sea urchins are also keystone structural species because they graze on the kelps and, in high enough densities, have the power to decimate areas of the kelp forests (Plate 7).

Plate 7 The sea urchin *Strongylocentrotus droebachiensis* is such a dominant functional species (grazing algae) that, if populations decline, the shallow community will change to one dominated by kelp forest. The reverse happens when populations expand leading to sea urchin barrens. See Hagen, 1987. Image: Sue Scott / JNCC.

Many temperate kelp habitats are characterized by a balance between the kelps and sea urchins. This relationship has been studied closely in Norway (eg Hagen, 1987; Christie and others 1995). Here, the northern sea urchin (*Strongylocentrotus droebachiensis*) is a significant grazer of the sugar kelp *Laminaria saccharina* and oarweed *Laminaria hyperborea* (also a kelp). High population densities of the northern sea urchin have left some areas completely devoid of macroalgae for decades (Christie and others 1995).

Such 'urchin barrens' are dominated by encrusting coralline algae, which the urchins do not consume. They also occur extensively in warm and temperate seas (see eg Valentine & Johnson, 2005; Micheli and others 2005). The grazing activity of the urchins in these areas is so high that macroalgae simply do not have a chance to grow since sporelings are grazed before they get a chance to reach a large size.

High mortalities of the green sea urchin during the 1990s made it possible to study the dynamics of the habitat without one of the keystone species. Christie and others (1995) noted that, at sites where there had been a significant decline in the numbers of sea urchins, there were dense stands of *Laminaria saccharina* within a few months. Experimental removal of urchins led to similar effects (Leinaas & Christie, 1996). At first, small filamentous algae and a few kelp recruits were observed. Luxuriant stands of *Laminaria saccharina* were established within a few months and after 2-3 years, the long-lived *Laminaria hyperborea* dominated. Urchin barrens have considerable resistance (Leinaas & Christie, 1996) and it would appear that it is changes in urchin populations rather than kelp populations that lead to balance shifts in kelp habitats.

It is likely that there is a complex interaction between sea urchin numbers, recruitment and predation. Populations of *Echinus esculentus*, for example, are probably controlled by several predators, parasites, disease and recruitment. Hagen (1987) linked the falling abundance of *Strongylocentrotus droebachiensis* in northern Norway to prevalence of a nematode endoparasite *Echinomermella matsi*. Vadas & Steneck (1995) proposed that urchin barrens in nearshore areas of the Gulf of Maine exist as a result of the overfishing of large predatory fish. These large predators would previously have fed on urchins (*Strongylocentrotus droebachiensis*), crabs and lobsters, therefore relieving predation pressure on the kelps. Due to the fact that large fish are now rare nearshore, areas that would previously have supported large stands of macroalgae have been replaced by urchins, crustaceans and encrusting coralline algae (Vadas & Steneck, 1995).

6.2 Identifying 'determining' and 'limiting' factors

In managing human activities to maintain marine ecosystems, it may be important to know what environmental and biological factors are essential or important to the maintenance of a particular species or community ('limiting factors') – and what factors are most likely to result in damage to or destruction of that species or community.

Environmental conditions and factors
Table 1 highlights some of the physical, chemical and biological environmental conditions that determine what sort of species assemblage species is present at a particular location and how rich or productive it is.

Table 1 Physical, chemical and biological factors that influence species assemblages

Physical	**Availability of suitable substratum**. Many species are highly specific in terms of selecting suitable substratum on which to settle. This is especially important when considering the recovery of populations following disturbance. For example, the barnacle *Bostrichia anglicum* only occurs on cup corals (Plate 8). The behaviour of the winkled rock borer (*Hiatella arctica*) is determined by substratum availability. Those settling on hard rock will attach by thread-like hairs and become nestlers while juveniles settling on soft rock become burrowers (Plate 9)
	Amount of suspended sediment
	Relative amounts of exposure to the air
	Temperature
	Turbidity
	Physical disturbance. Many species are intolerant of regular physical disturbance and areas subjected to it may be characterised by opportunistic fast-growing species such as encrusting bryozoans and serpulid worms. Intermediate disturbance often leads to high diversity (see section 6.9) (Plate 10).
	Wave exposure and water flow rate. Wave exposure can be responsible for relatively high levels of physical disturbance, especially during storms. Some species flourish in exposed habitats whereas others thrive in sheltered locations (Plate 11). Inshore residual currents affect suspended sediment and the distribution of chemical contaminants and propagules etc.
	Ocean currents. The NE Atlantic thermohaline circulation (the Gulf Stream) carries warm water northwards in the eastern Atlantic keeping our shores warmer than those at equivalent latitudes in the western North Atlantic
Chemical	Chemical pollutants
	Salinity
	Levels of dissolved oxygen
	Availability of nutrients
Biological	The presence of microbial pathogens
	The introduction of invasive species

Plate 8 *Bostrichia anglicum* (arrowed) on *Caryophyllia smithii*. The barnacle only occurs on cup corals and will be absent if corals are absent. Image: Keith Hiscock

Plate 9 *Hiatella arctica* is a nestling and boring species: on soft rock and in peat, it may be abundant and the holes that it leaves behind when individuals die are important in providing shelter for other species. Image: Keith Hiscock.

Plate 10 Only a few attached organisms can survive on mobile cobbles – they are fast growing, disturbance-tolerant species that settle rapidly or that grow readily from remaining parts after abrasion finishes. Image: Keith Hiscock.

Plate 11 Why such a rich abundance of species occurs in some habitats is often difficult to identify but shelter from the destructive effects of extreme wave action (because of aspect of the coast or depth) and the presence of moderate tidal currents, bringing suspended food, on rocky substrata often leads to the presence of rich communities. Knoll Pins, Lundy. Image: Keith Hiscock.

6.3 Variability with time

Variability with time occurs at a wide range of periodicities. Seasonal variability in the presence and abundance of species is marked especially in reproductive cycles. It is also true of the abundance of some benthic species, especially ephemeral algae, and in a wide range of pelagic species from phytoplankton to fish. Longer term variability may also occur in cycles with periods of a few years to decades and be difficult to predict.

Figures 11-13 highlight both short- and long-term fluctuations in the abundance of some species found within British waters.

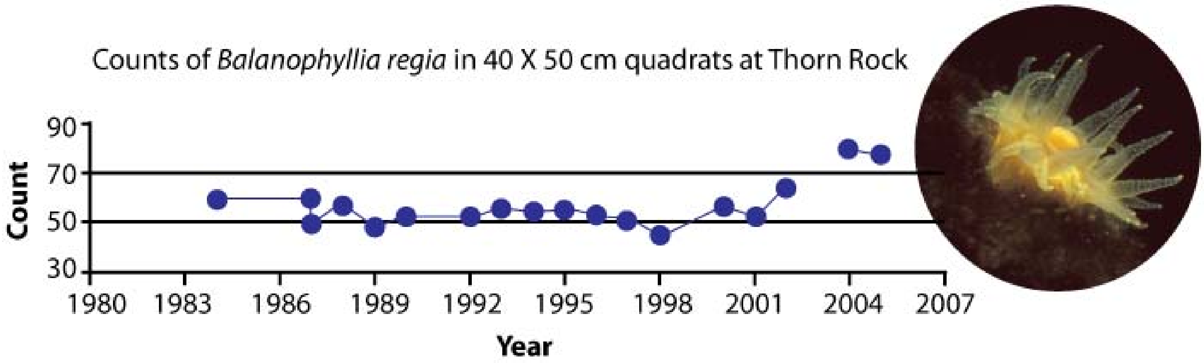


Figure 11 Long-term constancy and possible recent increase in the numbers of the scarlet and gold star coral at Thorn Rock, Skomer. From: Lock and others 2006. Image: Keith Hiscock.

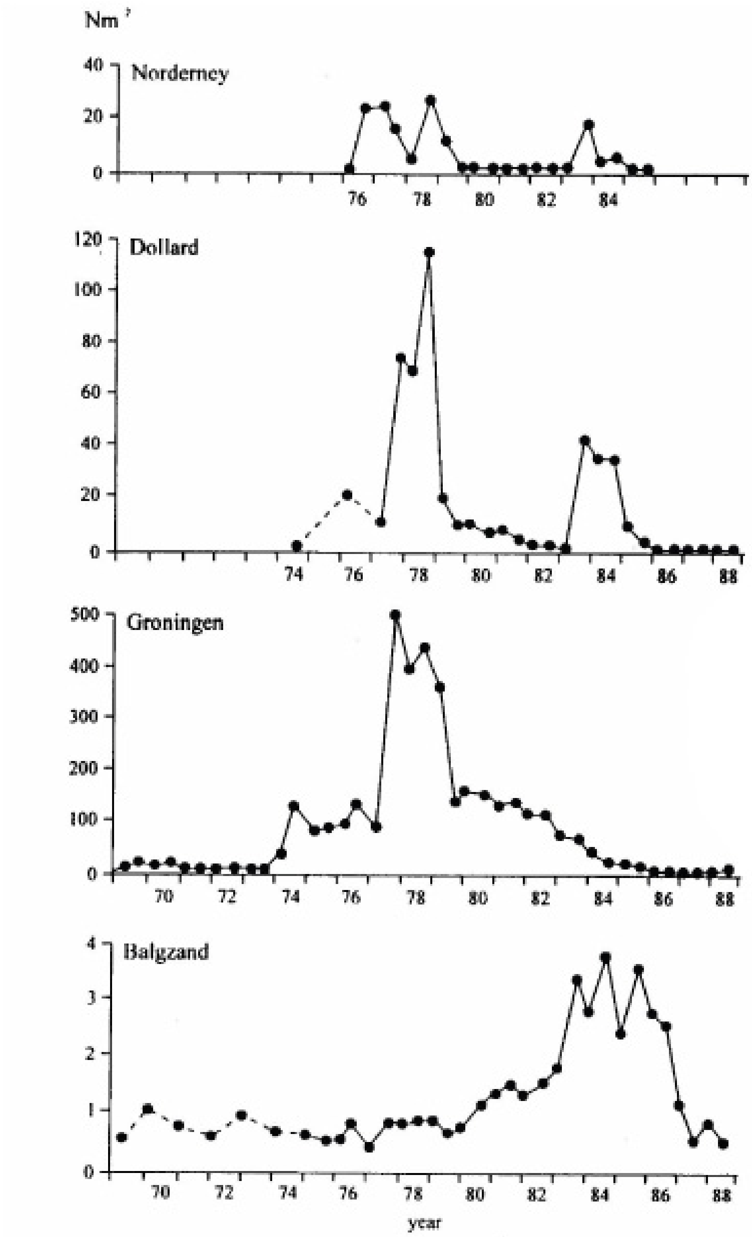


Figure 12 Some species show large annual changes in abundance. Average numerical density (per m^2) of the bivalve *Scrobicularia plana* at sites in the Wadden Sea over 20 years (redrawn from Essink and others 1991).

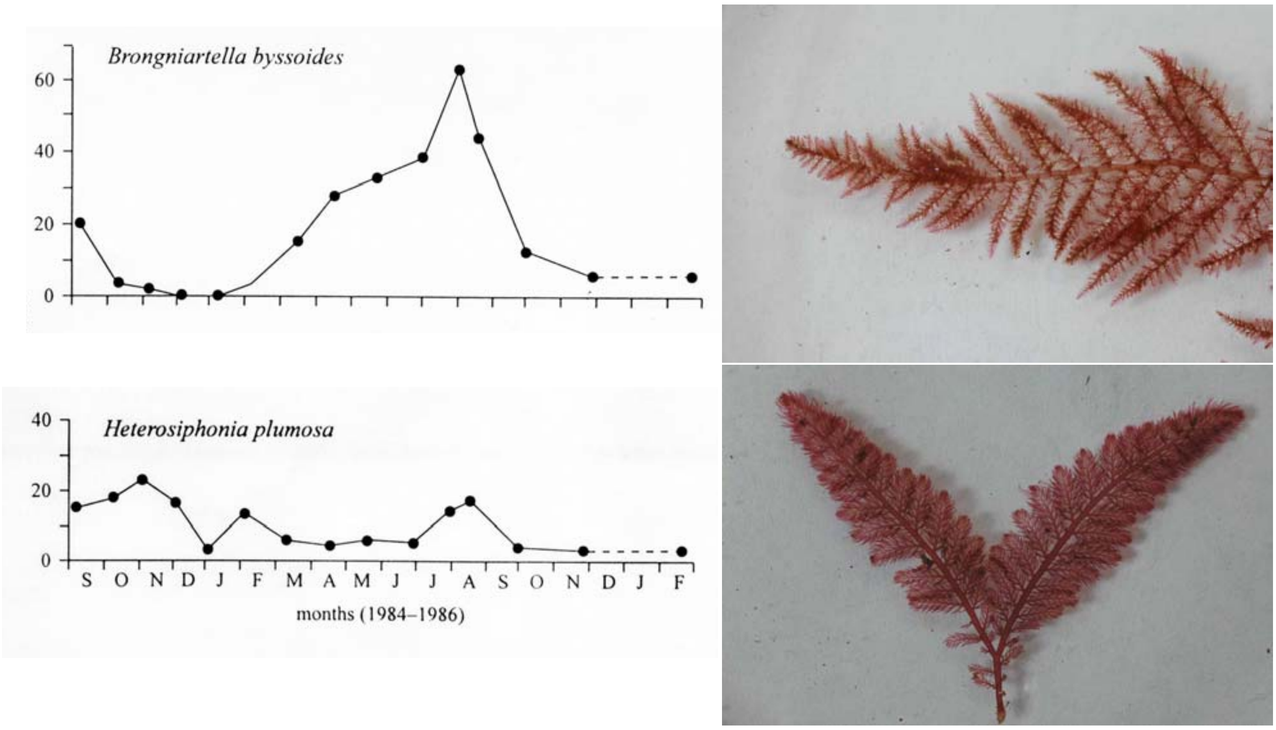


Figure 13 Seasonal fluctuations can be very marked. In the records for two algal species from stones at Skomer, *Brongniartella byssoides* has particularly large seasonal changes in abundance. From: Hiscock, 1986.

In British waters long-term changes in the relative abundance of species of intertidal barnacles have been recorded between the 1930s and 1950s, with cold water species declining in response to a rise in mean sea temperature of the order of 0.5 °C (Southward & Crisp, 1954) (see Figure 14). Subsequently, further changes were observed, including an increase in the northern species during a period of falling temperatures from 1962 to 1980 and then its decline as warming was resumed (Southward, 1991).

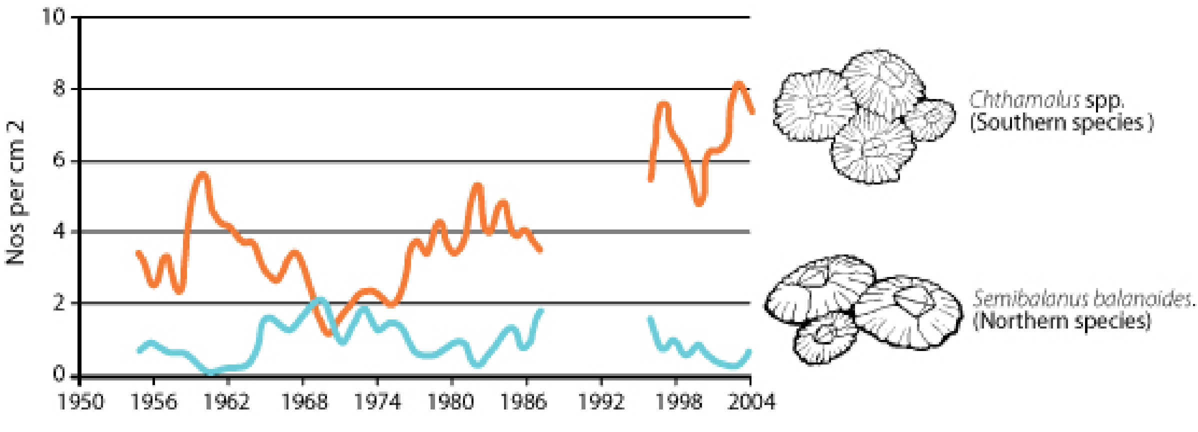


Figure 14 Long term changes in the abundance of two intertidal barnacles, *Chthamalus* spp. and *Semibalanus balanoides* from the midshore. Adjusted from Southward and others 2005. Barnacle drawings: Jack Sewell.

Pelagic species, especially fishes, are more sensitive to climate change than benthos and demersal fish. In the western English Channel, the relative abundance of herring and pilchard has fluctuated in response to climate over the past 400 years, the pilchard being dominant during warmer periods (Southward and others 1988) (Figure 15). These changes have been called the “Russell Cycle”, which is broadly linked to climate (Southward, 1963; Cushing and Dickson, 1976; Southward, 1980, Hawkins and others 2003). Corresponding changes are reported for other parts of European seas (Alheit and Hagen, 1996).

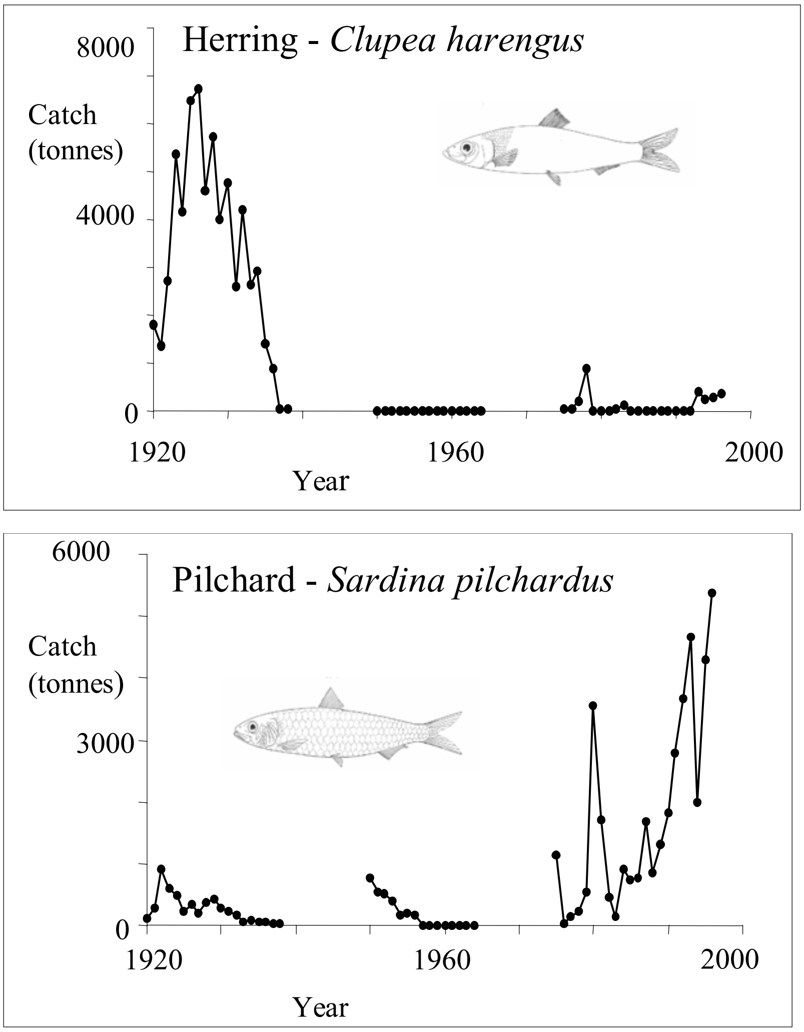


Figure 15 Catch data illustrating the relative abundance of herring (*Clupea harengus*) and pilchard (*Sardina pilchardus*) over the past eighty years. From Hawkins and others 2003. See also Southward and others 1988.

Any true long-term change is likely to be obscured initially by:

- short-term changes driven (for instance) by the decadal but irregular cycle of the North Atlantic Oscillation (Hurrell, 1995);
- the 11-year cycle of sunspot activity (Southward and others 1975; Southward, 1980), and
- longer-term fluctuations such as the Russell cycle (Russell, 1973; Cushing and Dickson, 1976; Southward, 1980; Hawkins and others 2003).

Short-term change is likely to be driven by:

- Physical disturbance of marine assemblages eg by winter storms;
- Grazing (as illustrated in Plate 12);
- Predation;

- Competition;
- High organic input including land runoff, plankton production, accumulation of plant detritus in still conditions where it rots, leading to de-oxygenation and the death of seabed organisms;
- The establishment of a seasonal thermoclines that isolates deeper water leading to de-oxygenation;
- High freshwater run-off that dilutes seawater and kills species highly intolerant of low salinity water;
- Extreme variations in temperature where maxima and minima determine the species that can survive and reproduce in an area, and
- Loss of facilitators.

Plate 12 If grazing species (limpets in the example illustrated) are excluded, fucoid algae become dominant within six months or a year (Hawkins, 1981; Jenkins and others 2005; Coleman and others 2006). Image: Stuart Jenkins & Steve Hawkins.

6.4 Variability across space: the importance of connectivity

Processes such as water movement, as well as the ability of some organisms to swim or walk, drives '**connectivity**', which is a very important feature of the marine environment. Different locations are likely to be 'connected' if:

1. water currents carry larvae/propagules or adults from one place to the other;
2. larvae or adults swim/walk from one place to the other, and/or
3. adults or larvae are carried from one place to another by human intervention.

Where larval dispersal is being considered, the longevity of the larva is of paramount importance in determining distance of connection. However, the biology is not simple. Larvae rise and fall in the water column, taking advantage of favourable currents, sheltering behind obstructions when unfavourable and, when ready to settle, 'testing' the seabed for suitability. That testing might be for chemical clues, that the sediment or geology is suitable or because adults of the same species are present there etc.

Degree of connectivity is important when considering whether or not recruitment will occur at a location which has been damaged and whether species will extend their distributions (for example as a result of seawater warming producing amenable conditions further north, or non-native species from their point of introduction). It is also important to determine degree of connectivity in relation to designing networks of marine protected areas (mpas) where each mpa is intended to support adjacent ones. Figure 16 highlights the limits of 'connectivity' of mainland populations of *Verruca stroemia* with relation to the Isles of Scilly.

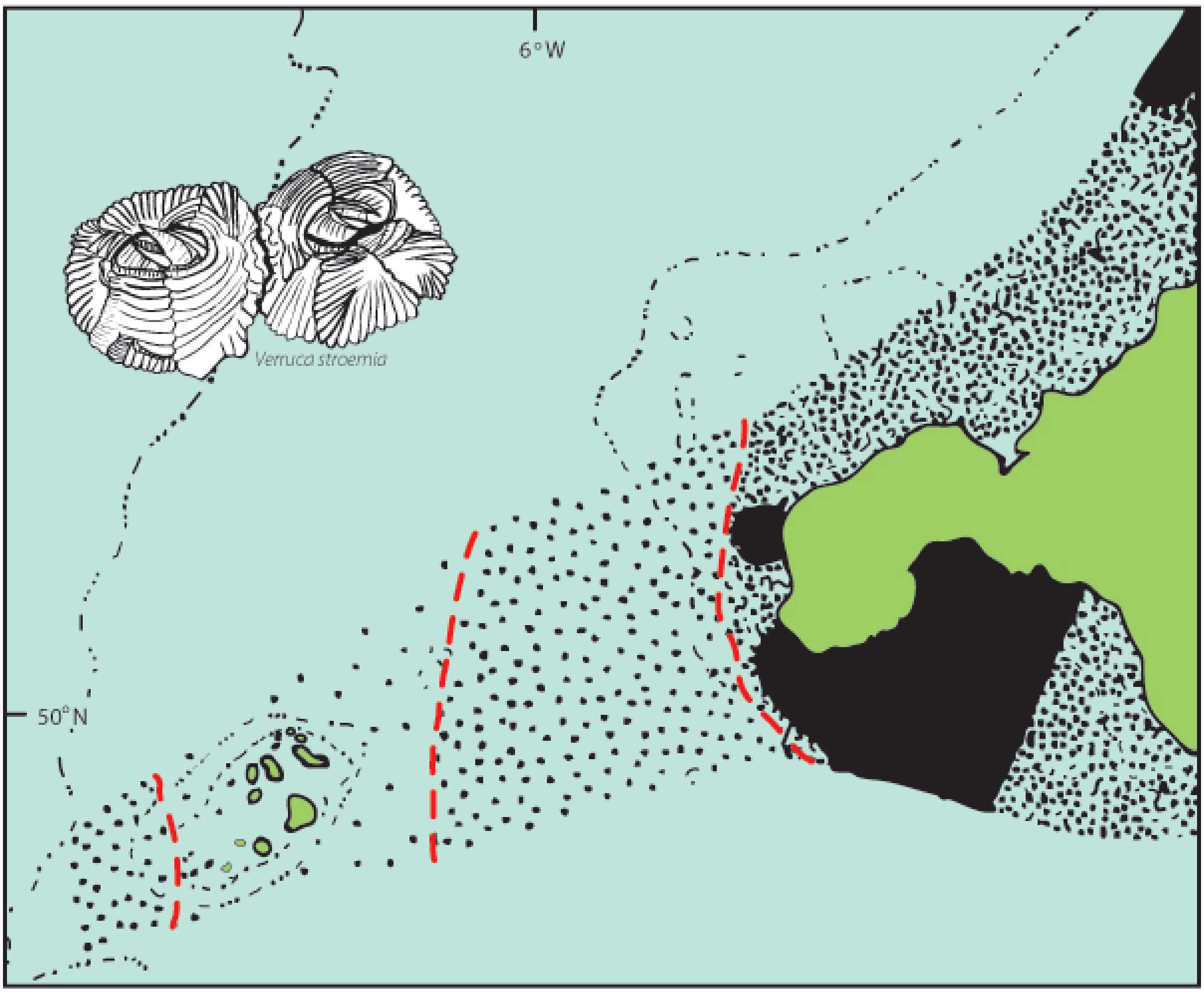


Figure 16 The abundance of larvae of the barnacle (*Verruca stroemia*) off south-west England. Larvae produced on the mainland do not drift sufficiently far to 'connect' with the Isles of Scilly where populations are small. Contours are at 10, 100 and 1000 individuals per 4 m^3 of water. Based on Southward (1962). Drawing: Jack Sewell.

Dispersal scales in marine species are extremely wide-ranging – from millimetres distance from the adult producing larvae or spores to hundreds of kilometres. Kinlan & Gaines (2003) reviewed the topic of propagule dispersal in marine and terrestrial environments and some of their results are illustrated in Figure 17. Approximately half the taxa that they considered are unlikely to populate locations further than 10 km away. Excluding fish, this is the majority of species of marine invertebrates and algae. Some larvae take only seconds after release before settling, some months. Larvae of the New Zealand spiny lobster *Jasus edwardsii* remain in the plankton for up to 2 years (Booth & Phillips, 1994) and recruits to New Zealand waters could come from Australian stocks (Chiswell and others 2003).

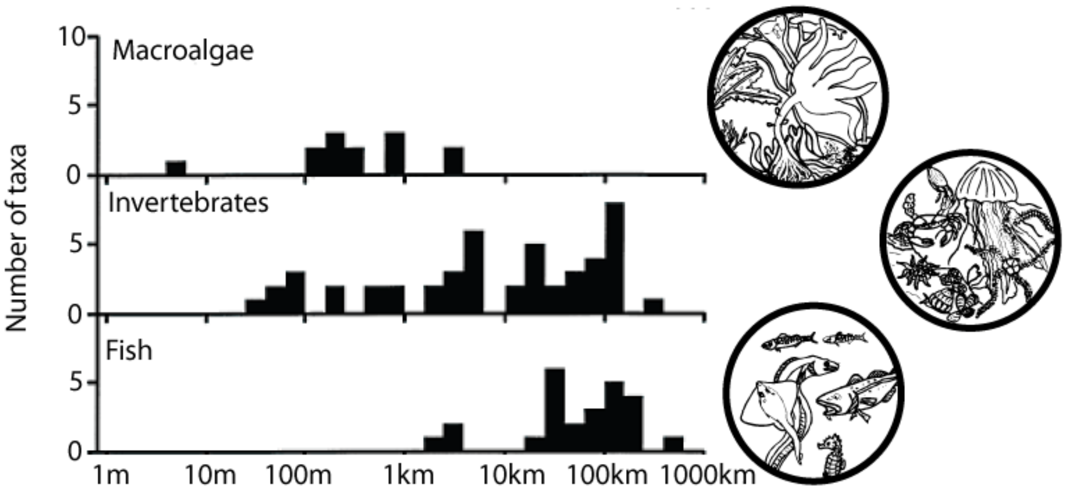


Figure 17 Distribution of mean dispersal distance estimates for marine benthic organisms. From Kinlan & Gaines (2003) with permission (Blackwell Publishing). Drawings: Jack Sewell.

Work undertaken recently in Lough Hyne in Ireland demonstrate how larval retention versus larval dispersal away from source can be difficult to predict and different from one location to another. Jessopp & McAllen (2005) noted that larval diversity within the Lough was distinct from surrounding areas suggesting that the Lough was not acting as a source or sink for larvae from areas outside the Lough. This discovery has implications for marine environmental management if marine reserves are to provide a source of larvae to surrounding areas (Jessopp & McAllen, 2005).

6.5 Variability across space – halo effects

For communities that are established and living as adults, there will be ‘spill-out’ from the particular habitat that they occupy. That spill-out will be particularly of mobile species that have refuge in the habitat under consideration and which may rely on surrounding areas for food (see Figure 18). The concept of halo effects is particularly important when determining boundaries of reef protected areas, although there are few observations to suggest how far species forage away from their refuge habitat.

6.6 Variability across space – ‘honey pot’ effects

The honey pot effect is most easily illustrated by a reef habitat where a combination of food and shelter attracts a wide range of fish and crustacean species. On a small scale, a dead fish will attract a temporary assemblage of scavenging species. Fish and crustaceans may also assemble at effluents where organic matter, perhaps including fish waste, is discharged.

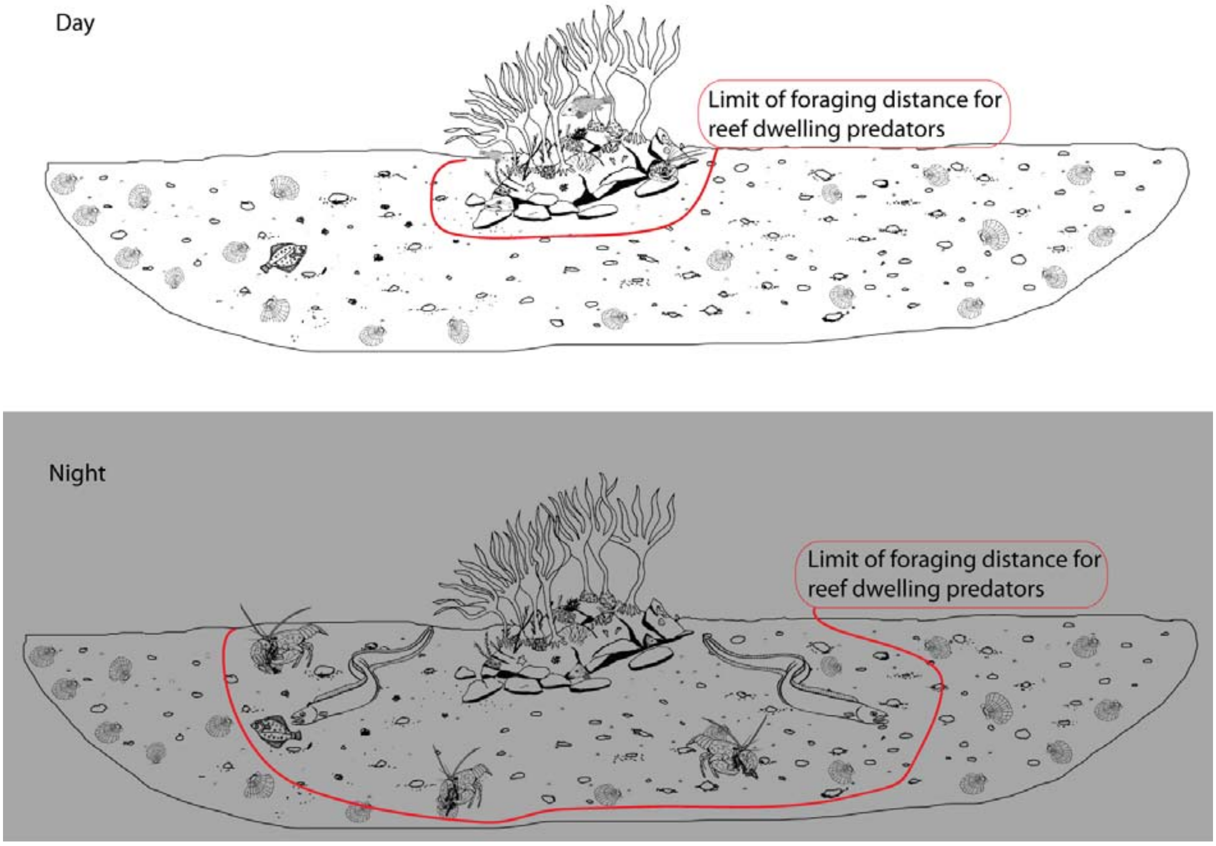


Figure 18 An illustration of how a halo effect might operate for a patch reef habitat. Nocturnal foraging by the common lobster (*Homarus gammarus*) and the conger eel (*Conger conger*) is used to demonstrate. Drawing: Jack Sewell.

6.7 Variability across space – 'special places'

Special places may be favoured locations to spawn or to refuge including at certain times of the year (Plates 13 and 14). In the case of fished species, once those special places are located, they may be subject to intense exploitation and/or protected to conserve stocks or breeding.

Some examples are:

- Areas where different water bodies meet (eg frontal areas, estuary mouths) are often areas of high nutrients and therefore places where food can be found.
- Spawning areas. Black bream (*Spondyliosoma cantharus*) find areas of seabed where shallow layers of sediment overlay harder surfaces and clear away the sediment to lay eggs. The resulting pits can be clearly seen on acoustic images.
- Refuges. Female dogfish will aggregate in rock holes, possibly to avoid unwelcome attention from males.
- Refuges. The space under boulders that are supported above the layer below provides a refuge from predation for crustaceans, worms, molluscs, echinoderms and for fish to lay eggs.

Plate 13 Female dogfish refuge in shallow water caves (Victoria Wearmouth, pers. comm.). The causes of this unisexual aggregation are currently being investigated at the Marine Biological Association of the United Kingdom. Image: Keith Hiscock.

Plate 14 Underboulders provide a refuge from predators. 'Nests' of the file shell, *Limaria hians* under a boulder at 20 m depth. Image: Keith Hiscock.

6.8 Process interconnections

Processes and environmental conditions act together to determine the sorts of marine communities that develop. For instance:

1. larvae may be distributed great distances but may not reach a stage able to settle if they are taken into areas too cold for final development (see Lindley, 1998);
2. residual currents distribute larvae of species that live attached to rocks but those larvae will have no-where to settle if the currents take them over sediments.

Such natural breaks in distribution as in 2. above may be breached as a result of construction of hard coastal defences, offshore wind farms etc. that provide 'stepping stones'.
See also section 6.4 (connectivity).

6.9 Bringing structure and processes together: supporting diversity

To understand patterns of biology in space and time and to be able to go some way to understanding how or why those patterns might change, our understanding of structure, function and processes needs to be brought together and summarised. A simplified diagram for species diversity is shown in Figure 19.

Understanding how high biodiversity (in terms of species richness) is created and (most importantly for management) is maintained is at the core of managing human activities to maintain or to restore that diversity (= "conservation"). Heterogeneity creates many niches for colonisation and is important. Supply of nutrients, light and food are also important. The amount of predation or grazing pressure will often determine richness. One of the most influential hypotheses in marine ecology has been the 'intermediate disturbance hypothesis'

(Caswell, 1978). The theory is best explained using boulders on the seashore as an example (see Sousa, 1979). Small boulders get moved around on almost every tide. As a result they might bash against others rocks, land upside down

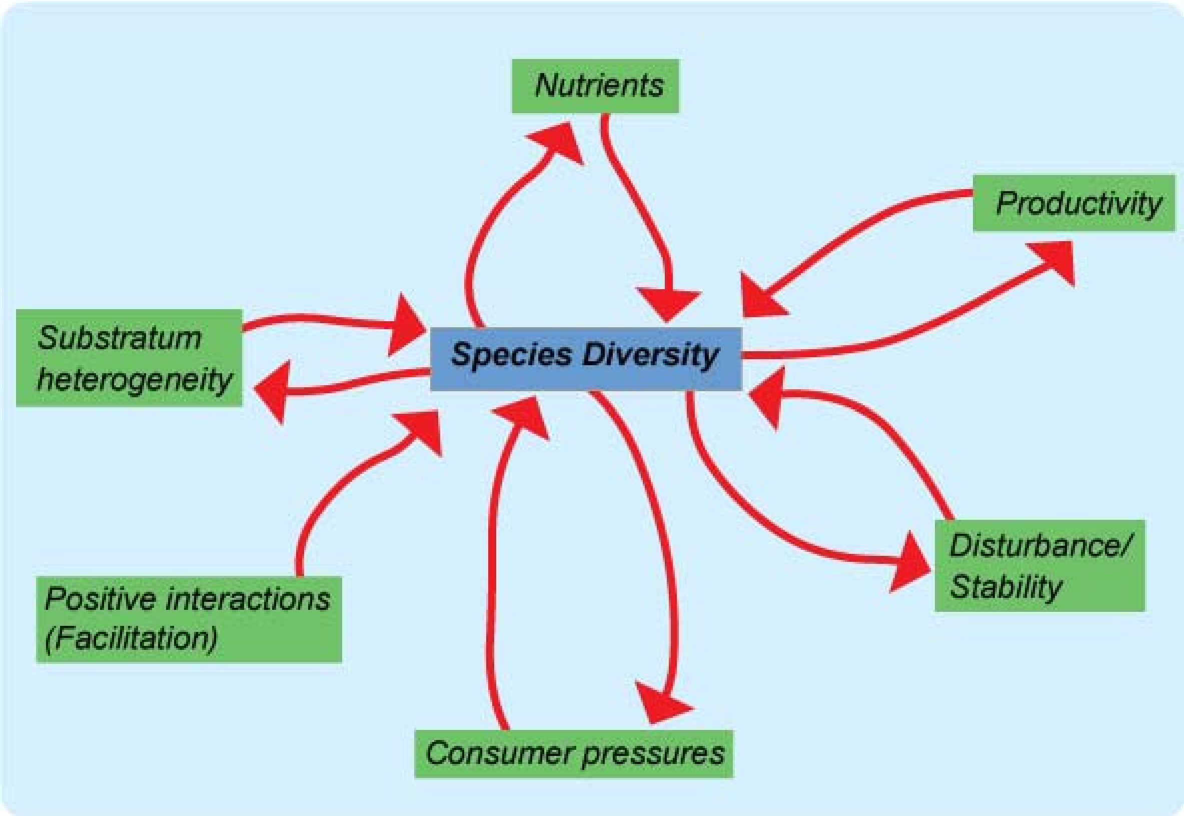


Figure 19 A simplified model of how structure and processes affect species diversity – and how species diversity affects structure and processes. Based on a diagram used by J. Stachowicz at the Benthic Ecology Meeting 2006.

and move into areas that are not necessarily ideal for the species living on them. Accordingly, the community on that small boulder will never get a chance to fully develop and will be characterized by a small number of species, probably not in very high abundance, that are tolerant of disturbance. At the other end of the spectrum, there are large boulders which will probably only very rarely get moved around, if at all. These boulders will have been stable for long enough that the abundance of species on them is probably much greater than on the small boulders. However, due to the greater stability afforded to these larger boulders, the communities on them tend to become dominated by a few species which occur in high abundance, resulting in low species richness. These dominating species will be competitively superior to other species in the area given the conditions of that area. The highest diversity will occur on boulders of an intermediate size since these gets turned occasionally. Succession is interrupted but the community starts off beyond the early pioneer stage (Raffaelli & Hawkins, 1999). Essentially this means that the community is given long enough to develop into a diverse species rich habitat but not long enough for a few competitively superior species to take over. 'Disturbance' may result from low-level grazing or predation, by disease or from other factors that will prevent one or a few species becoming dominant.

In environmentally stable situations where space in the community is not dominated by a few competitively superior species and where predators are not in high abundance, species richness may be high because of that stability. The longer that a habitat remains undisturbed by extreme environmental conditions, the more species will settle and survive, including the low abundance species, many of which may only recruit infrequently but live for a long time. These are 'biologically accommodated communities' and the large number of species that occur in such communities is accounted for by the 'Stability-Time Hypothesis' of Sanders (1969). Such rich communities can be seen in deeper or wave-sheltered sublittoral sediments and on hard substrata where wave action and tidal currents are only moderately strong.

7 Sustaining biodiversity and ecosystem services

7.1 Introduction and summary of likely effects

Environmental change occurs naturally but it is the adverse effects of human activities that need to be managed. When assessing the impact of a particular activity it is not only necessary to look at changes in the affected communities of species and their environment in a particular area, but also to take into account how such changes may result in effects elsewhere. Table 2 summarises some of the likely effects of human activities on processes and therefore patterns.

Table 2 Environmental factors that may be affected by human activities (*MarLIN* factors) with equivalents in the 'Pressures' used by the Environment Agency. For a detailed appraisal of likely effects of each factor on species and biotopes visit www.marlin.ac.uk

Environment Agency Pressures	*MarLIN* Factors	Examples of likely effects on ecosystem structure and functioning
	Substratum loss	Loss of species and the subsequent loss of sediment stability provided by them eg seagrass or *Sabellaria* reef loss.
	Smothering	Loss of filtering function if filter feeders are smothered and cannot feed.
Suspended sediment	Increased suspended sediment	Possibility of increased scour which may reduce the number of species attached to rock.
	Decreased suspended sediment	Reduction in ability of *Sabellaria*, and other species that require sand, to build tubes.
Increased turbidity	Increased turbidity	Less light for primary productivity resulting in reduced micro- and macroalgal growth.
	Physical disturbance	Loss of important physical structure including habitats such as biogenic reefs. Change of sediment structure.
	Synthetic chemicals	Poisoning of larvae. Interference with reproductive ability of gastropods leading to population decline.
	Heavy metals	Death of echinoderm larvae leading to a reduction in species function eg grazing.
	Hydrocarbons	Loss of grazers from intertidal areas leading to increased macroalgal abundance.
Priority substances	Changes in nutrients	Phytoplankton blooms resulting in increased turbidity and reduced sediment oxygen levels.
Salinity	Increased salinity	Death of organisms with low tolerance to change in optimum, for them, salinity.
	Decreased salinity	
	Degree of fluctuation in salinity	

Environment Agency Pressures	*MarLIN* Factors	Examples of likely effects on ecosystem structure and functioning
Oxygen concentration	Deoxygenation	Loss of infauna resulting in reduced bioturbation and nutrient cycling.
Thermal range/heat	Increased temperature	Extended spawning period for some species.
	Decreased temperature	Cold intolerance leading to death.

7.2 Case studies - how human activities disrupt natural properties, structure and functioning of marine ecosystems

Disruption of natural properties, structure and functioning of marine ecosystems by human activities may have minor to severe consequences. In many cases, the character of the disruption will be obvious but in many cases, it will not. Often, it is unclear if some apparently disastrous event has been brought-about or contributed to by human activities.

7.2.1 Case study 1. Decline in mussel beds and associated biodiversity in southern California – a possible result of global warming

Sea water temperatures along the southern California coast have increased since 1976. Whilst it is uncertain if that warming is the result of the natural Pacific Decadal Oscillation or is a part of wider global warming, the increased temperature has had severe consequences for the mussel beds along the coast. It seems most likely (Smith and others 2006) that warmer temperatures have led to increased stratification of waters (both 'properties'), isolating the deep nutrient rich waters so that, in turn, zooplankton biomass has been reduced (by 80% between 1951 and 1993: Roemmich & McGowan, 1995). Mussels are filter feeders and rely on zooplankton for food. Mussels have declined in thickness and extent (affecting structure) whilst associated species richness in the mussel beds has declined by about 60%. Mussels are also important as an energy link between the pelagic system and benthos (functioning), providing a wide range of predators with food.

7.2.2 Case study 2. Mussel bed development due to nutrient enhancement

Carreg Walltog, south of Cardigan Bay in Wales, is a muddy sand habitat with large boulders. In 1995 the boulders supported a diverse community including dense dahlia anemones (*Urticina felina*) with patches of sponges and sea squirts on large overhangs (JNCC, 1999). Following several years of high nutrient effluent from a nearby shellfish factory, the site is now almost completely dominated by common mussels (*Mytilus edulis*) (Rohan Holt, pers. comm.). Mussels will now dominate the habitat for at least several years. The diversity of the previous community has been lost and the nature of the mussel matrix means that the nature of the sediment will have been altered. For example, the build up of faeces, pseudofaeces, and trapped sediment underneath the mussels may lead to increased anoxia to the detriment of much of the infaunal community (see Plate 15). Reversion to the previous community, even if the mussels are lost, seems unlikely unless the high nutrient effluent stops.

Plate 15 The mussel *Mytilus edulis*. When mussel beds become established, they can dominate the seabed and completely change the nature of a habitat. Image: Sue Scott.

7.2.3 Case study 3. The declining importance of seagrass beds

Seagrass beds are characterised by high productivity and biodiversity and are considered to be of great ecological and economic importance (Davison & Hughes, 1998; Asmus & Asmus, 2000 a, b) (Plate 16). Seagrass plays an important role in the stabilization of many intertidal and subtidal areas due to the network of rhizomes (roots) produced by the plants. However, the extent of seagrass (*Zostera marina*) beds has greatly decreased since the 'wasting disease' which decimated seagrasses on both sides of the Atlantic during the 1920s and 1930s (Nybakken, 2001). The source of the disease remains unclear but 'disease' is one of the factors likely to affect processes. The decline in seagrasses resulted in loss of the functional and structural contribution made by the leaves which had previously slowed currents and encouraged the settlement of fine sediments, detritus and larvae (Orth, 1992). The diverse infauna associated with the beds provide an important food source for intertidal fish and birds. The decline of *Zostera marina* beds in Europe and North America in the 1920s -30s also caused Brent geese (*Branta bernicla*) to shift their diet to *Zostera noltii*, which is now their preferred food (Davison & Hughes, 1998; Jones and others 2000). Wigeon (*Anas penelope*) numbers have also declined dramatically in recent years, presumably due to the loss of their food, *Zostera marina*.

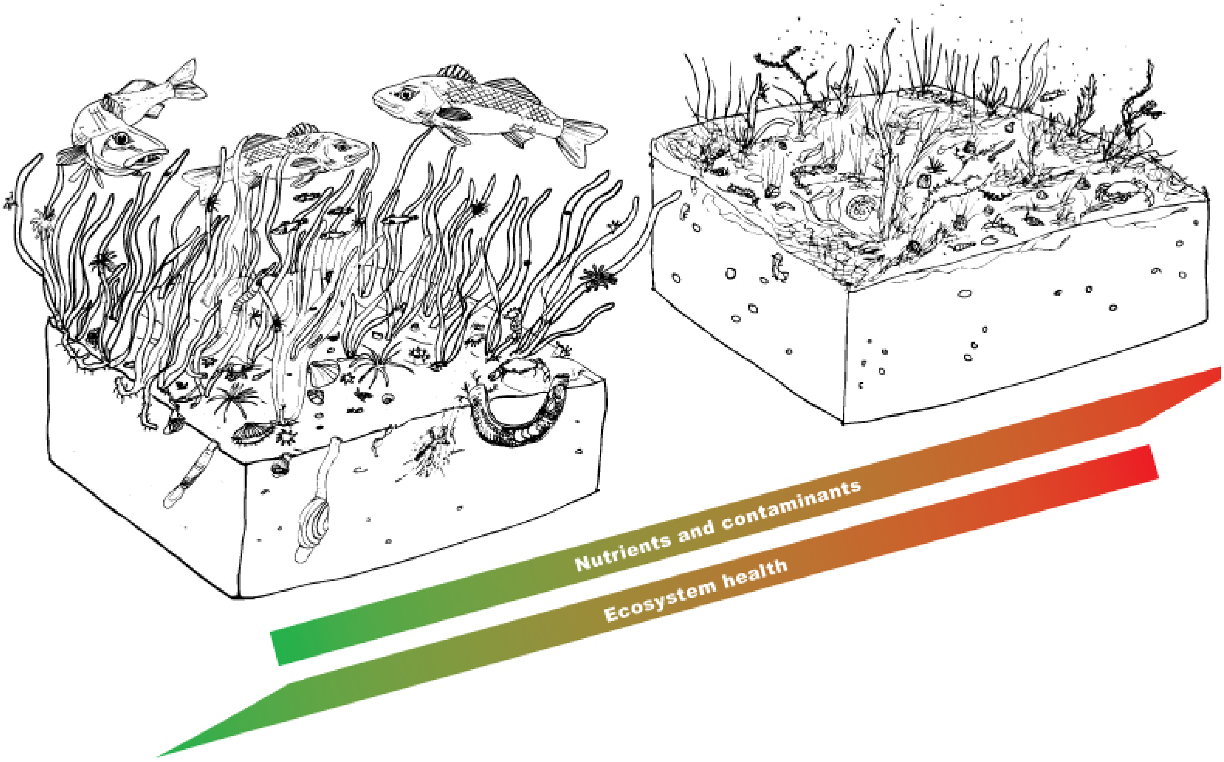
Plate 16 Seagrass beds such as this one characterised by high biodiversity and productivity and are considered to be of great ecological and economic importance. Image: Keith Hiscock.

Seagrass beds are subject to various anthropogenic disturbances. Activities leading directly to the loss of seagrass beds may include dredging and dumping. Indirect factors include aquaculture, pollution, building causeways and possibly overfishing. The fact that overfishing could potentially lead to the loss of seagrass beds (Hughes and others 2004) is ironic given that the beds can play a key role in protecting the early life stages of commercial fish species. Figure 20 highlights some of the biological, chemical and physical parameters underpinning the health of seagrass beds.

Eutrophication has often been suggested as a common factor in the loss of seagrass beds worldwide. Based on 35 other seagrass studies, Hughes and others (2004) reported that nutrient enrichment in the water column, and an associated increase in epiphytes, had a strong negative effect on seagrass biomass. Algal epiphytes can limit light and nutrients getting to the seagrass blades, to their detriment. Den Hartog (1994) reported the growth of a dense blanket of *Ulva radiata* in Langstone Harbour in 1991 that resulted in the loss of 10 ha of *Zostera marina* and *Zostera noltii*. The fast growing filamentous algae completely smothered the seagrass leading to the decay of the underlying algae and subsequent deposition of sulphurous material on the sediment. By the following summer, the *Zostera* sp. were completely absent, although this may have been exacerbated by grazing by Brent geese.

In addition to the loss of seagrass, the common cockle *Cerastoderma* edule, previously highly abundant, was lost from the area and had also not recovered by the following summer. These are not only a valuable commercial species but are also burrowers whose activity contributes to the oxygenation of the top 2 cm of sediment, thereby reducing the percentage of active sulfate reducing bacteria (Mermillod-Blondin and others 2004). Algal blooms can also shade out the seagrasses. In the absence of nutrient enrichment, large macroalgae tend to dominate because they are competitively superior with regard to low nutrient levels, they have good internal nutrient cycling and they can access nutrient pools in the sediment (Duarte, 1995). In contrast, fast growing macroalgae and phytoplankton invariably dominate in response to nutrient enrichment because they are closer to the water's surface and can use light better. As seagrasses die off, this results in an increase in sediment loss which led to a further influx of nutrients to the water column therefore further enhancing phytoplankton growth.

Hughes and others (2000) found that the ragworm *Nereis diversicolor* had a negative impact on the growth of shoots of the seagrass *Zostera noltii*. Ragworms have been seen to increase in abundance following eutrophication (eg Beukema, 1989) and are tolerant of nutrient enriched habitats and moderate levels of hypoxia (Diaz & Rosenberg, 1995). If this was true, the re-establishment of seagrass beds following loss from eutrophication could be further hampered by the presence of large numbers of the ragworm.



Healthy and diverse seagrass bed		**PHYSICAL & CHEMICAL FACTORS**		**Degraded seagrass bed**
Low	←	Mechanical disturbance	→	High
Moderate	←	Water flow rate	→	Low / stagnant
Low	←	Turbidity	→	High
Very low	←	Siltation	→	High
Optimum	←	Temperature	→	High
Low	←	Dissolved nutrients	→	High
Low	←	Chemical contaminants	→	High
High / variable	←	Salinity	→	Low

BIOLOGICAL FACTORS

Low	←	Disease	→	High
Low	←	Epiphytes	→	High
High	←	Small grazers (snails etc.)	→	Low
Low	←	Large grazers (birds)	→	High

Figure 20 Factors likely to determine the health of a seagrass (*Zostera marina*) bed. Drawings: Jack Sewell. Original concept: Keith Hiscock.

7.2.4 Case study 4. Introduction of non-native toxic algae

Boalch (1979) describes how, in the early autumn of 1978, and over a short period of time, reports were received of 'red tides', dead and dying fish, death of intertidal and bottom fauna, death of caged fish, abnormally high catches of some species and collapses of some shellfish catches, from various locations on the south Cornish coast. Similar experiences were reported in along the south and south-west coats of Ireland (Cross & Southgate, 1980) leading to massive kills of grazers and subsequent algal proliferation.

At the same time, Boalch (1979) received reports that the dinoflagellate *Noctiluca scintillans*, capable of forming slicks or 'red tides', was abundant in coastal waters in the western English Channel. Furthermore, both water and surface sediment sample revealed high concentrations of the non-native dinoflagellate *Gymnodinium aureolum* (now *Karenia mikimotoi*) (Plate 17). The decaying cells from the bloom could have reduced oxygen levels in the near-bottom waters or led to the clogging of benthic organisms although it is not known if this was the causes of the 'fish kill' (Boalch, 1979).

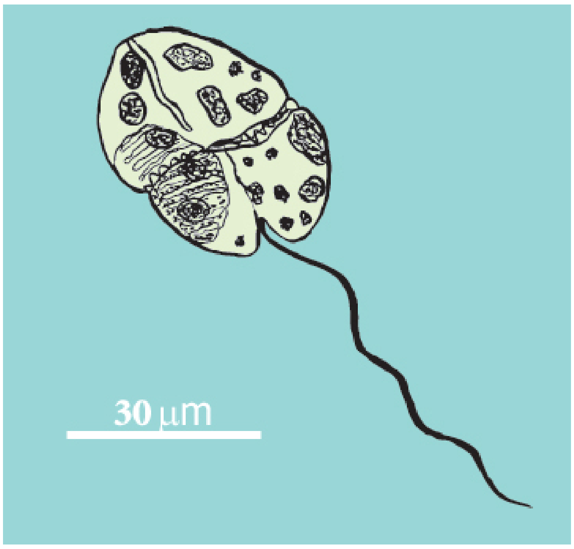


Plate 17 The dinoflagellate *Karenia mikimotoi* (previously *Gymnodinium aureolum*). In high abundances, dead and decaying cells from this organism may lead to reduced oxygen levels and invertebrate and fish kills. Drawing: Jack Sewell.

Plate 18 Fish and invertebrates killed by a bloom of the non-native dinoflagellate alga *Karenia mikimotoi* (previously *Gymnodinium aureolum*) in Killary Harbour in July 2005. Image: Rohan Holt.

A similar event occurred on the west coast of Ireland in 2005, resulting in fish kills, death of benthic organisms and evacuation of the seabed by organisms that were able to escape (Plate 18). The following quotation is from the British Marine Life Study Society bulletin:

"I dived Killary Harbour (a long enclosed sea lough)….only to find that all the brittlestars in what was an extensive bed; large molluscs including whelks and scallops; all starfish, all fish (everything from blennies, gobies, butterfish, flatfish etc) and many of the infaunal species - (worms, priapulids, sea cucumbers), were either dead and rotting, or gaping and unresponsive. The only animals that seemed to be hanging on were the common hermit crabs and the organ-pipe worm, *Serpula vermicularis,* which were still extending their tentacles from their calcareous tubes but retracting them quickly when we approached. On another dive in the upper reaches of Kilkieren Bay a 'population' of the fireworks anemone *Pachycerianthus multiplicatus*, were notably moribund and would not retract their tentacles nor retreat into their tubes when disturbed." Dr Rohan Holt.

7.2.5 Case study 5. Fishing and trophic cascades

Worm and Myers (2003) have presented evidence to suggest that the loss of Atlantic cod has resulted in cascading effects lower down the food chain, so called "top-down" control. The removal of large numbers of cod has meant that its benthic prey species ie crustaceans including northern shrimp (*Pandalus borealis*), snow crabs (*Chionoecetes opilio*) and American lobster (*Homarus americanus*) have increased in abundance (Worm & Myers, 2003). Commercially, northern shrimp is a highly important species with important fisheries throughout the Atlantic. There is an intensive fishery around Iceland and a most important one off the Norwegian coast (FAO, 2004). In the Kattegat and Skagerrak it is fished for by Danish trawlers and, in the northern and central North Sea Danish, Norwegian, British, German and Dutch trawlers fish for the species (FAO, 2004).

According to the Worm & Myers (2003), cod and shrimp biomass time series data revealed strong inverse relationships in seven out of nine populations, suggesting that the removal of the predator in this food chain has led directly to an increase in prey abundance. These cascades have been reported for other species that cod feeds on including herring, which feed on cod eggs and larvae (Garrison & Link, 2000; Köster & Möllman, 2000; Frank and others 2005). An increase in the abundance of species that feed on cod eggs could further inhibit the recovery of cod (Worm & Myers, 2003). Figure 21 illustrates how reducing cod populations can increase predation on cod eggs and cause a negative feedback impact on cod numbers.

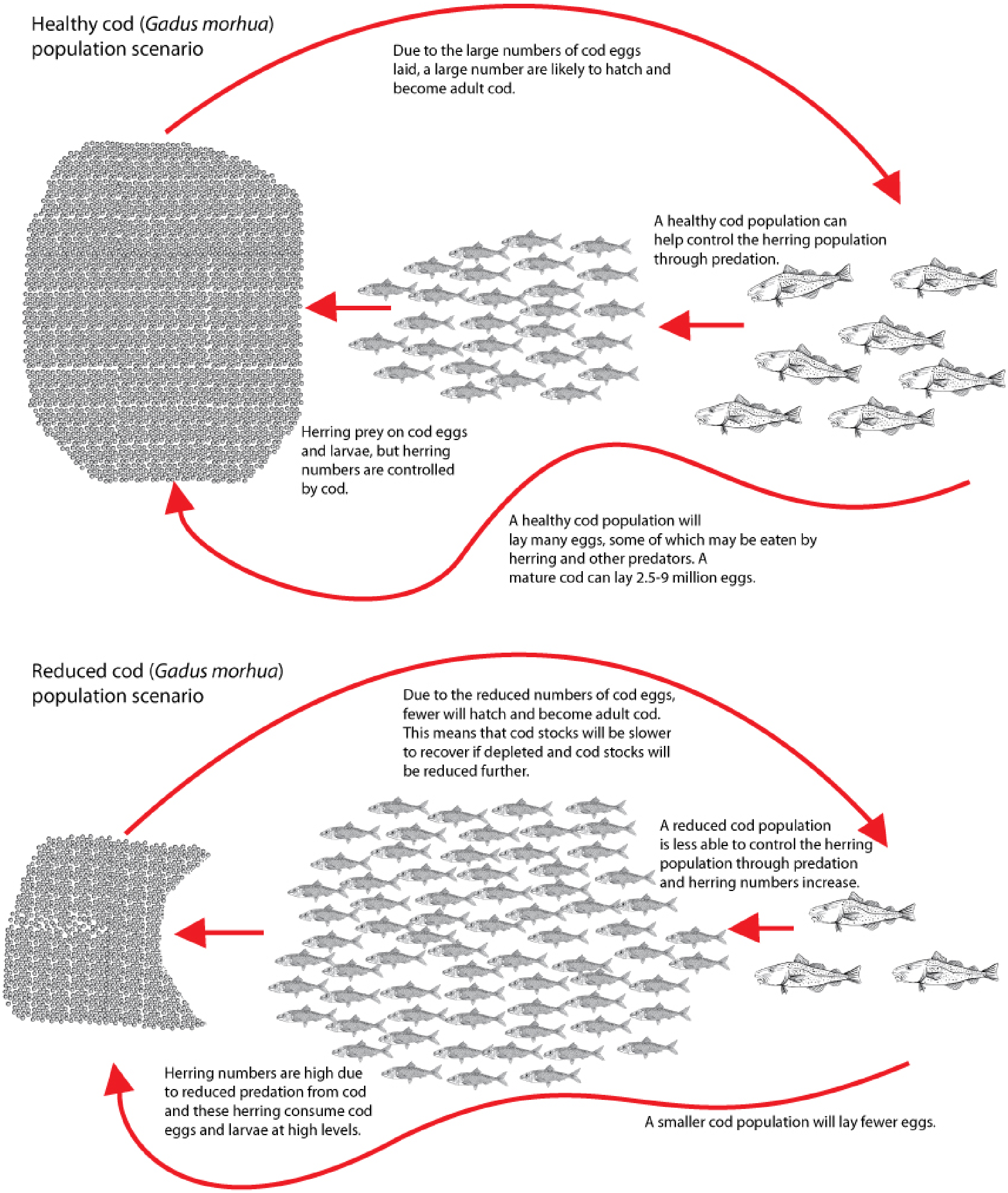


Figure 21 How reducing cod populations can increase predation on cod eggs and cause a negative feedback impact on cod numbers. See, for example, Frank and others 2005. Drawings: Jack Sewell.

7.2.6 Case study 6. Long-term changes in seabed species composition influenced by fisheries

Much evidence exists to suggest that bottom fishing can have long-term impacts on the benthos of fished areas (eg Lindeboom & de Groot, 1998; Frid and others 1999; Rumohr & Kujawski, 2000). Demersal fisheries can affect benthic habitats in a number of ways including reducing infaunal diversity and loss of large and fragile species.

Rumohr & Kujawski (2000) studied benthos in the southern North Sea. They compared historical data from the beginning of the 20th century to data from 1986. The most obvious change over time was a drastic reduction in the number of bivalve species. Eleven bivalve species, including *Phaxas pellucidus, Ensis siliqua* and *Thyasira flexuosa,* were not found again in the 1986 samples. In contrast, many scavengers and predators, including the common starfish (*Asterias rubens*), common whelk (*Buccinum undatum*) and swimming crab (*Liocarcinus holsatus*), had experienced marked increases in abundance and distribution within the sites. It is thought that these large shifts are as a result of fisheries impacts, including discards and moribund benthos on the seafloor, which would have increased the availability of food for both predators and scavengers (Rumohr & Kujawski, 2000). Several echinoderms including the sea potato (*Echinocardium cordatum*), the brittlestar *Ophiura albida* and heart urchin (*Brissopsis lyrifera*), also experienced a marked increase in abundance. Many other studies, both short- and long-term point to increase in the abundance of scavengers / predators as a result of this increased food availability.
For example, Frid and others (1999) compared the macrofauna between a Dublin Bay prawn (*Nephrops norvegicus*) fishing ground off the Northumberland coast and a site outside the ground over 25 years. They reported increases in some species of errant polychaetes, starfish and brittlestars during periods of high fishing intensity within the fishing ground. The abundance of these species also decreased with fishing intensity suggesting that fishing activity was directly responsible for such changes. Furthermore, the site outside experienced changes in macrofauna as a result of increased organic input. This was also true of the site within the fishing ground although this influence broke down with the commencement of the period of high fishing activity, again suggesting that fishing activity was influencing the dynamics of macrobenthos (Frid and others 1999).

7.2.7 Case study 7. Effects of reducing structural complexity because of fishing

Habitat homogenisation happens when structural habitats (for instance rock reefs) or species (for instance, horse mussel *Modiolus modiolus* beds) are damaged or destroyed by physical disturbance such as by mobile fishing gear. In such situations, species richness is reduced as a result of:

- mortality of fragile species;
- loss of habitat-specific species (where the habitat is destroyed);
- loss of refuges amongst structurally complex habitats, and
- impossibility of replacement where long-lived, slow growing species with direct development or benthic larvae have been destroyed.

Homogenisation of habitats risks loss of ecological function and natural heritage values. Losses may also reduce resilience thereby predisposing the system to sudden and dramatic change. Figure 22 illustrates the loss of structural complexity as a result of the effects of scallop dredging on maerl beds. Growth and development of unattached maerl thalli from crustose individuals is very slow and likely to take in the order of several decades for a bed to form.

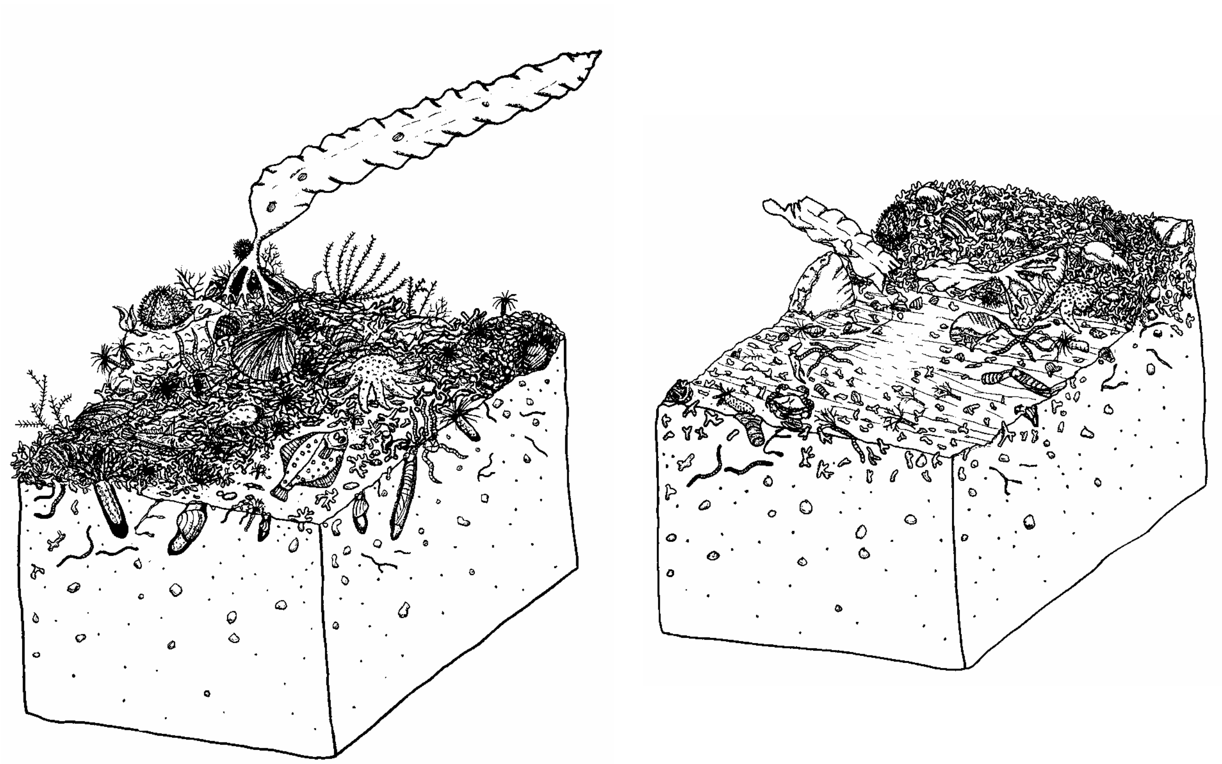


Figure 22 Live maerl (right) *Phymatolithon calcareum*, (a slow growing calcareous red seaweed), provides a structure for other species to nestle in, hide amongst and attach to, so creating a high diversity of species. Scallop dredging may significantly reduce the number of species, number of individuals and lower the biomass of macrofauna (left) (Pranovi and others., 2000). Maerl beds can be destroyed by trawling or dredging (eg Hall-Spencer & Moore, 2000). Drawing: Jack Sewell.

7.2.8 Case study 8. Effects of removing filter feeders by fishing impacts

The loss of horse mussel (*Modiolus modiolus*) beds resulting from scallop dredging in Strangford Lough represents loss of structure with consequence for ecosystem functioning. Not only did the beds provide a habitat for many different species as a result of their physical structure but the transfer of energy from the plankton to benthic species through filter feeding and the production of faeces as fine sediment, for example, are important functions for the community.

The loss of high throughput filter feeding species can have severe implications, especially in enclosed waters where algae blooms may be more likely to occur. The value of benthic suspension feeders in controlling phytoplankton biomass has been documented (eg Cloern, 1982; Officer and others 1982). Control is through the filtering activities of the suspension feeders which can, in sufficient numbers, prevent the build up of excess organic material in the water column. Officer and others (1982) reported that San Francisco Bay has no obvious light, temperature, nutrient or turbidity limiting conditions for phytoplankton growth. The area receives large nutrient inputs including effluent from 20 sewage treatment plants yet the area is characterised by low phytoplankton biomass from May to December (Cloern, 1982) and not by substantial seasonal blooms characteristic of eutrophic areas. The benthic population is dominated by clams and mussels (Officer and others 1982) and these suspension feeding bivalves are in sufficient quantity that their filter feeding activities can control the phytoplankton biomass (Cloern, 1982).

Haamer and others (1999) reported a shift from large to small phytoplankton as water passed over a mussel bed in Sweden. This altered phytoplankton community contained almost no dinoflagellates (some species of which can produce dangerous toxins). Moreover, the mussel bed led to enhanced primary production as a result of improved light conditions and nutrient release from the mussel bed (Haamer and others 1999).

In Chesapeake Bay, eastern USA, the functioning of the ecosystem has changed dramatically over the past century. Chesapeake Bay has historically been the home to large biogenic oyster reefs containing numerous other suspension feeders (Kirby & Miller, 2005). However, Rothschild and others (1994) reported a more than fifty-fold decline in the oyster population in the Maryland area of Chesapeake Bay since the early part of the 20th century, which they attributed mainly to the mechanical destruction of the beds and stock overfishing. The use of large oyster dredgers and hydraulic-powered patent tongs has meant that many formerly productive areas are now covered in silt. Since 1860, *Crassostrea virginica* have also experienced slower growth rates (Kirby & Miller, 2005). The deterioration and loss of oyster reef habitat has lost with it the important suspension feeding function in the Chesapeake Bay ecosystem. The loss of filtration by oysters and the biogenic habitat that they create is suspected to be the reason for increasing eutrophication and alteration of food webs in Chesapeake Bay (Luckenbach, 2002) and the increasing frequency, magnitude and duration of dinoflagellate blooms in Chesapeake Bay (Luckenbach and others 1993).

7.2.9 Case study 9. Bad timing – the case of trophic mismatch

During the 20 years leading up to the early 1980s, Atlantic cod (*Gadus morhua*) experienced huge abundance in the North Sea. The reason for their success was complex but the planktonic climate, on which they are so dependant during the early stages of their lives, was highly favourable. Food was in abundance meaning that greater numbers than normal survived the perilous early life stages. Cod rely on various different food sources from the moment they hatch. In the North Sea, cod eggs start to hatch in March / April (Cushing, 1990). From then on their fate is strongly determined by the availability of a sequence of different sources of prey. The larvae at first feed on copepod eggs, progressing to euphausid nauplii within a couple of months. The diet then consists primarily of copepods until euphausiids and other fish larvae dominate it from August (Thorisson, 1989). Quite simply, if the food is not available then the likelihood of the larval cod maturing is slim. Timing is essential because the prey species are only abundant at certain times of the year and the hatching of the larvae is closely coupled with the greatest abundance of prey species.
There is now evidence to suggest that large scale shifts in the seasonality of plankton in North Sea have occurred (Beaugrand and others 2002; Beaugrand and others 2003; Edwards & Richardson, 2004; Edwards and others 2006). Rising sea surface temperatures since the early 1980s have been seen to change the planktonic climate in such a way that is detrimental to the survival of young cod (Beaugrand and others 2003). Such changes have been part of an overall 'regime shift' for the North Sea which has been well documented. A regime shift in the marine environment has been defined by de Young and others (2004) as "*changes in marine system functioning that are relatively abrupt, persistent, occurring at a large spatial scale, observed at different trophic levels, and related to climate forcing*". A significant regime shift in the zooplankton community has been reported as recently as 2000 (Edwards and others 2006). The late 1980s regime shift in the North Sea occurred at a time when the North Atlantic Oscillation (NAO) shifted from a negative to a positive phase. Essentially, this means that there was a greater amount of warm water entering the north of the North Sea from the Atlantic and that resulted in changes in the ecology of the North Sea at all trophic

levels in the pelagic from the 'bottom up' (Alheit and others 2005). 'Bottom up', in this respect, means that the changes were brought about as a result of the phytoplankton responding to the changes caused by the NAO switch. Due to the fact that the phytoplankton are at the bottom of the food chain, changes in their ecology will have ramifications at higher trophic levels.

Data collected during the Continuous Plankton Recorder survey has revealed some alarming trends in the plankton ecosystem (Beaugrand and others 2003; Edwards & Richardson, 2004; Edwards and others 2006). Firstly, the mean size of calanoid copepods has decreased by a factor of two since the beginning of the 1980s. Secondly, the calanoid *Calanus finmarchicus* has been progressively substituted by *Calanus helgolandicus* (Beaugrand and others 2003). As a result, the timing of the occurrence, and hence availability as food, of *Calanus* has been delayed by several months and no longer coincides with the time when cod larvae need to feed on them. A reduction in prey availability will ultimately lead to reduced survival and may lead to poor recruitment. Such plankton fluctuations have been found to be significantly related to changes in sea surface temperature in the North Sea and these changes in the relative abundance of the copepod species have contributed to a decline in North Sea cod (Reid and others 2001; Beaugrand and others 2003).

In addition to changes in the phyto- and zooplankton, changes in the benthos and other fish species, including catches of the western stock of horse mackerel *Trachurus trachurus*, have been reported (Reid and others 2001; Alheit and others 2005).

7.2.10 Case Study 10. The increasing abundance of lobsters in the North Sea

Numbers of the common lobster *Homarus gammarus* appear to have increased dramatically on the North Sea coast of England in recent years. The popular view is that because the numbers of cod have declined, they are no longer eating young lobsters. A larger increase in lobsters (the American lobster *Homarus americanus*) has also occurred on the Atlantic coast of Canada. However, in Canada, exceptionally few lobsters are found in the guts of cod and it seems most likely that young (small) lobsters are benefiting from consuming the bait that is used to trap them (and then exiting the trap) and possibly from increased temperature. The American lobsters have also started to live in sedimentary habitats where they did not significantly occur before – possibly because of crowding in reef habitats. (From a presentation by Stanley Cobb at the Benthic Ecology Meeting 2006).

7.2.11 Case study 11. Fishing down the food web: replacement of large predatory fish with jellyfish

There is evidence to suggest that over fishing in the Atlantic could explain some huge increases in the abundance of jellyfish (Lynam and others 2006). Lynam and others (2006) have studied populations of jellyfish off the Namibian coast and estimate that the biomass of jellyfish is now more than three times that of commercially viable fish such as anchovy and sardine which have, over the past 50 year or so, been over-fished. These fish species would normally compete with the jellyfish for food and the reduction in their abundance has benefited the jellyfish. This change has been predicted as a consequence of 'fishing down the food web' (Lynam and others 2006). The jellyfish population, once established may result in further pressure on the fish stocks for two reasons. Firstly, they have few predators (meaning that numbers could increase further, depending on other factors such as food, temperature etc) and secondly, the jellyfish prey on the eggs and larvae of fish (Lynam and others 2006).

Similar problems have been documented in the Black and Caspian Seas where the invasive comb jelly *Mnemiopsis leidyi* has had dramatic and catastrophic effects on the ecosystem (see eg GESAMP, 1997; Finenko and others 2006).

8 Taking account of random (stochastic) events

Significant change can occur as a result of events that, whilst the events are predictable, when they will occur is not. Such events include:

1. severe or prolonged storms (Plates 19 and 20);
2. predator invasions (Plate 21);
3. disease (Plates 22 and 23), and
4. massive recruitments (Plate 24).

Other random events are less easy to predict or anticipate occurring. for instance, non-native species are arriving around Britain increasingly frequently but when (or if) a species that devastates native fauna will arrive is unknown.

Plate 19 Severe or prolonged storms may displace sediment infauna and attached epifauna. Image: Keith Hiscock.

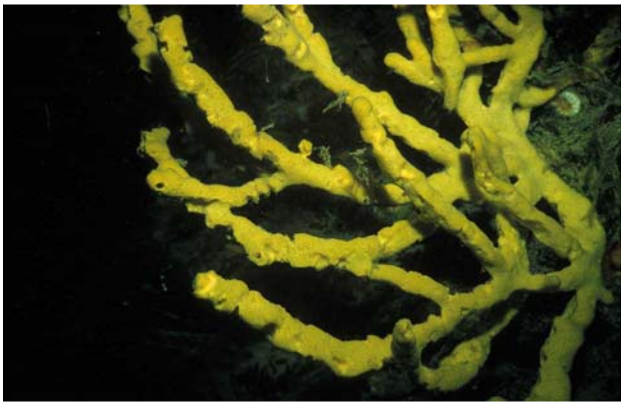


Plate 20 In 1977, prolonged easterly gales damaged many long-lived and slow-growing sponges at Lundy. Image: Keith Hiscock.

Plate 21 Mussel beds are periodically destroyed by 'fronts' of common starfish *Asterias rubens* due to massive recruitments. Image: Sue Scott.

Plate 22 In 2001, the population of sea fans at Lundy was decimated by a mystery disease – a similar event was recorded at Plymouth in 1924. Image: Keith Hiscock.

Plate 23 In 1988, Phocine Distemper Virus decimated populations of seals (especially common seals where over 50% died in The Wash) – if the virus re-occurs, populations could again decline. Image: Keith Hiscock**.**

Plate 24 Some species with planktonic larvae may rely on occasional 'jet stream' currents to populate new areas. The purple sea urchin *Paracentrotus lividus* occasionally 'turns up' in south Devon, the Isles of Scilly and the Hebrides. Image: Sue Scott.

9 The role of resistance, resilience and recovery in maintaining baseline conditions

9.1 Introduction: how far can you 'push' an ecosystem before it collapses?

Can scientists identify when natural of human pressures will cause an ecosystem to cease to function properly or cease to be viable as a supplier of goods and services? Or, are policy makers expecting too much of marine scientists? An engineer can predict what weight of trucks it would take to cause a bridge to collapse, so why cannot a marine scientist predict when an ecosystem will collapse?

The amount of resistance, resilience and recovery (Box 5) potential that a species, community or habitat has determines when an ecosystem ceases to function properly or ceases to be viable as a supplier of goods and services.

Box 5
Resistance: The tendency to withstand being perturbed from the equilibrium (Connell & Sousa, 1983).
Resilience: The ability of an ecosystem to return to its original state after being disturbed (from Makins, 1991) (cf. 'constancy', 'persistence', 'stability').
Recoverability: The ability of a habitat, community or individual (or individual colony) of species to redress damage sustained as a result of an external factor.
Stability: The ability of an ecosystem to resist change (from Makins, 1991)

9.2 Stability theory

The stresses that affect ecosystem processes are many and complex. We assess the impacts of those stresses through field experiments and through observation and measurement when disaster strikes. Estimating how far you can push an ecosystem before it collapses (and what it will change to) is, however, more likely to be expert judgement than through some mathematical calculation because of non-linearity.

Some communities (represented by the ball in Figure 23a) may switch to other communities after large scale disturbance but may return to their original state after a period of stability (see section 9.3.1). Communities on cobbles on the open coast may develop to a stable assemblage of species but become ‘turned-over’ and destroyed after a major storm that might happen only every few years).

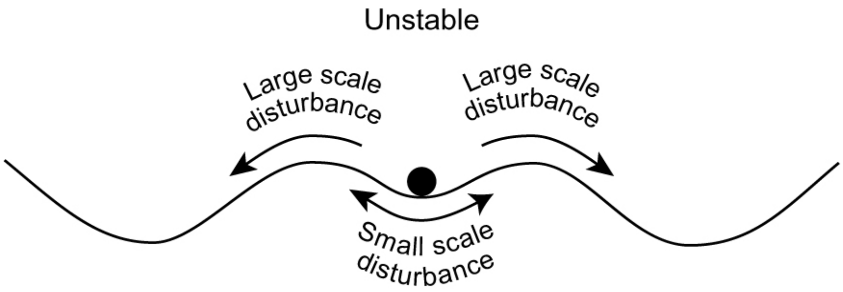


Figure 23a Some communities are inherently fragile and may not be expected to persist in the face of even small-scale disturbance. Small scale disturbance makes small changes to the community (illustrated as a ball that may move within the limits of the hollow it is in) but returns to the entity. Large scale disturbances are likely to change the community to something different, although return to the previous community is possible. Adapted from Gray 1977.

Some communities (represented by the ball in Figure 23b) may persist over long periods of time with only minor variation in composition. After normal disturbance their resilience will permit a return to the previous state; ie they are able to withstand shocks and to re-build themselves if damage has occurred. However, an abnormal disturbance may destroy species that, because of longevity and unlikely recruitment, will not recover. Such events may result in extinction of that community and colonisation by some different and persistent community (see section 7.2.11).

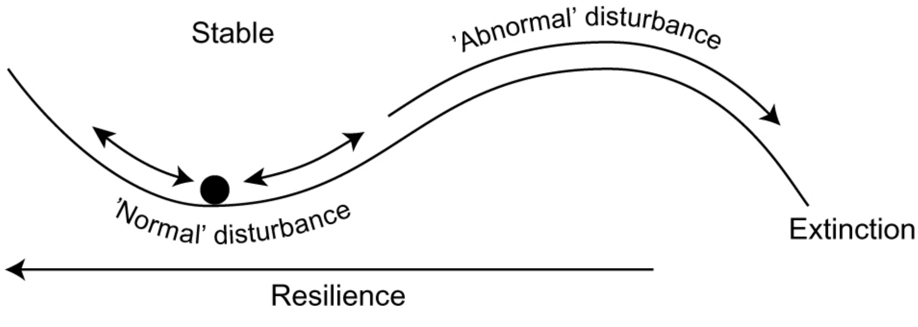


Figure 23b Abnormal disturbance may destroy communities that are not able to resist; for instance those that are characterised by long-lived, slow growing species. Adapted from Gray 1977.

It is important to try to understand how communities will respond to disturbances or changes in disturbance regime. Box 6 details some of the questions that need to be answered when predicting the effects of events and activities within the marine environment.

Box 6

Predicting the effects of events and activities
The following are the sorts of questions – whether he/she knows it or not – that a marine biologist with environmental management experience probably goes through when delivering an expert judgement on the likely effect of an event or activity:

1. What environmental factors will the event or activities influence?
2. How strong is the effect of the changing factor?
3. Is there any synergy with other change occurring?
4. Will one factor change another (knock-on effects)?
5. For how long is/has the changed factor occurred?
6. Will any key structural or functional species be exterminated?
7. How long can the community resist change (is there redundancy in structural and functional species)?
8. How quickly, if at all, can the community recover (will the community be replaced by a different stable community, has the physical and chemical habitat reverted to previous state etc.)?

9.3 Resistance and resilience

9.3.1 Case study 12. Nutrients and rocky shores

Bokn and others (2003) demonstrated how increasing the quantity of nutrients in the seawater of a rocky shore experimental mesocosm (Plate 25) failed to drive significant change to the community compared to control tanks where no nutrients were added over the first three years. However, during the fourth year of nutrient enrichment, the cover of fucoid algae started to decline and they crashed in the fifth year (probably as a result of old fucoid individuals dying and not being replaced in the treated mesocosms) (Kraufvelin and others 2006). Green algae had apparently taken-over. Resistance had come from the combined effects of competition for space and light imposed by canopy-forming algae and grazing on opportunistic algae. That resistance had failed when canopy algae and gastropods had died. After a further two years on regular seawater, the macroalgal and animal communities had returned to within the range of normal variability (showing a high level of resilience).

Plate 25 Experimental studies where nutrient levels have been increased over rocky shore communities at Solbergstrand revealed a delay of about three years before significant effects of increased abundance of opportunistic algae were observed. The delay was because existing ecosystem processes such as grazing resisted the ascendancy of the opportunistic algae. (See Kraufvelin and others 2006.).

9.4 Recoverability

The potential for a species, biotope or for a whole landscape feature to recover – to return to its former state – depends on many of the characteristics of species described previously. For recovery to occur, there has to be:

1. The same or similar habitat still present. Habitat includes substratum, water quality and physical processes.
2. A source of propagules or mobile adults or juveniles near enough to recolonize.

Recovery may follow a successional process that means that it will take some time for something close to the original community to develop. “Some time” might be months or more likely several years. Figure 24 provides a graphical indication of the time taken for certain rocky shore species to recover from an oil spill. The recovery of a rocky shore and saltmarsh following an oil spill is also visually represented in Figure 25 and Plate 26 respectively.

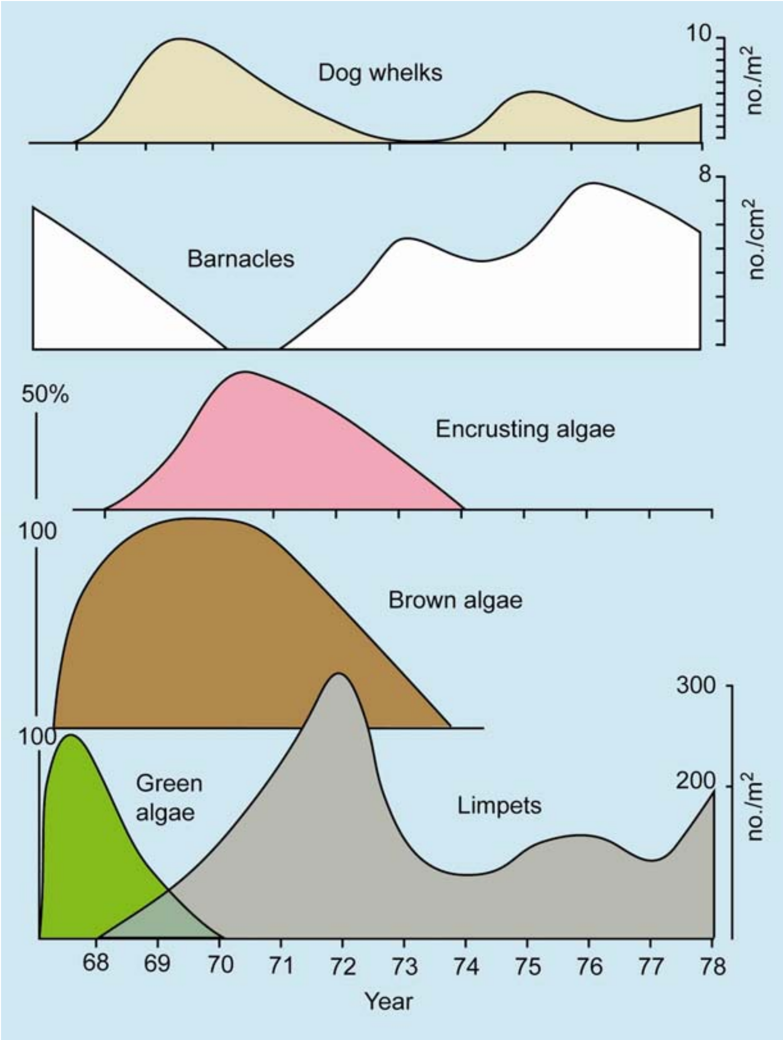


Figure 24 Studying recovery following accidents can help us to predict likely recovery rates from future events. Changes in the abundance of some common shore species following the *Torrey Canyon* oil spill (March, 1967). Based on: Southward 1979. See also Hawkins & Southward, 1992**.**

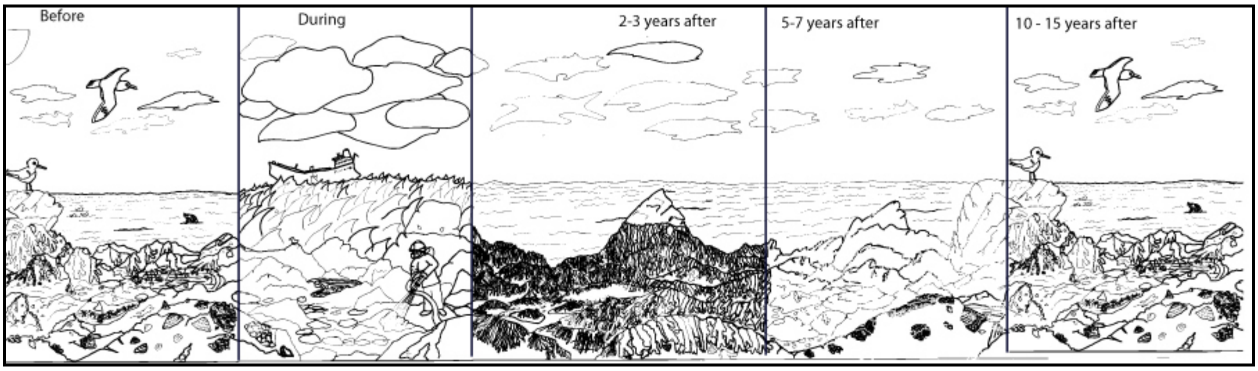


Figure 25 Diagram illustrating the different appearances of a moderately exposed rocky shore in the years following an oil spill.

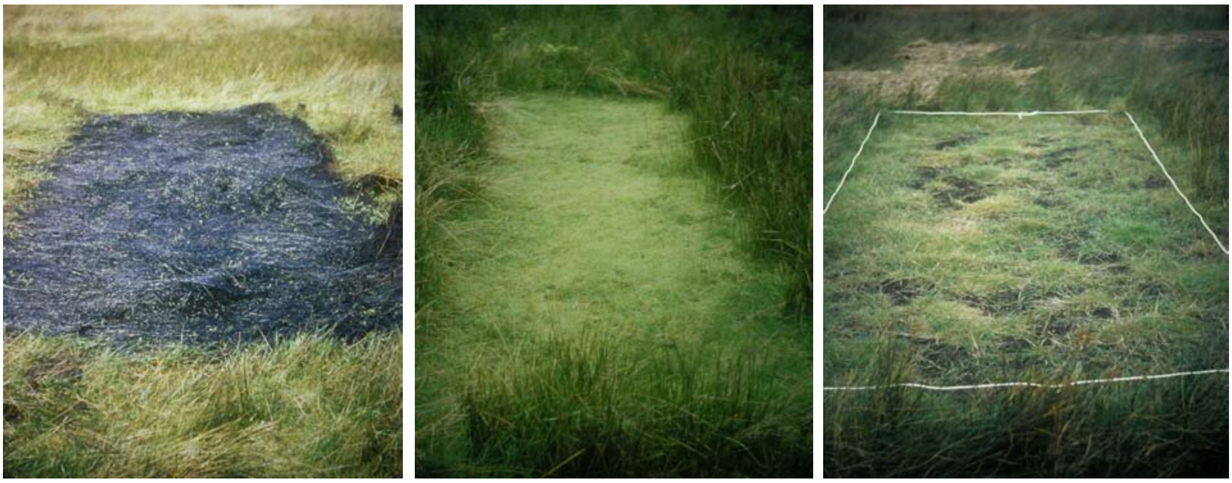


Plate 26 Experimental studies help us to predict likely recovery rates from accidents and events. Oiled saltmarsh plots. See Baker (1976). Image: OPRU/Jon Moore.

The length of time that recovery is likely to take is of fundamental importance in assessing 'sensitivity' of species and communities to environmental perturbations. The sensitivity of species and communities can be identified from the *MarLIN* Web site.

The *MarLIN* programme researches sensitivity (intolerance and recovery potential) of species and biotopes. Table 3 lists the biotopes that span the range from low to very high sensitivity to various factors.

Table 3 Biotopes that have both low and very high sensitivity to certain environmental perturbations. Estimates of likely establishment or recovery rates are indicated. Establishment and recovery rates assume local source of larvae for species with short-lived larvae. The biotope names are from the Marine Biotope Classification (Version 97.06).

Biotope name	Factor(s) to which it is very or highly sensitive	Recovery
Ceramium sp. and piddocks on eulittoral fossilized peat	Substratum loss	Recovery is not possible from factors to which the biotope is very or highly sensitive
Fucoids and kelps in deep eulittoral rockpools	Introduction of non-native species	
Seaweeds in sediment (sand or gravel)-floored eulittoral rockpools	Introduction of non-native species	
Yellow and grey lichens on supralittoral rock	Substratum loss Displacement Synthetic compound contamination Hydrocarbon contamination	Partial recovery from factors to which the biotope is very highly sensitive is only likely to occur after about 10 years and full recovery may take over 25 years or never occur.
Zostera noltii beds in upper to mid shore muddy sand	Change in wave exposure Displacement Change in nutrient levels	
Erect sponges, *Eunicella verrucosa* and *Pentapora fascialis* on slightly tide-swept moderately exposed circalittoral rock	Substratum loss Abrasion & physical disturbance Displacement Change in salinity	

Biotope name	Factor(s) to which it is very or highly sensitive	Recovery
Modiolus modiolus beds with hydroids and red seaweeds on tide-swept circalittoral mixed substrata	Substratum loss Synthetic compound contamination Decrease in salinity Extraction	Partial recovery from factors to which the biotope is very highly sensitive is only likely to occur after about 10 years and full recovery may take over 25 years or never occur.
Lophelia reefs	Substratum loss Change in temperature Abrasion & physical disturbance Extraction	
Halcampa chrysanthellum and *Edwardsia timida* on sublittoral clean stone gravel	Increase in water flow rate Increase in wave exposure	
Lithothamnion glaciale maerl beds in tide-swept variable salinity infralittoral gravel	Substratum loss Smothering Desiccation Change in emergence regime Abrasion & physical disturbance Extraction	
Phymatolithon calcareum maerl beds with hydroids and echinoderms in deeper infralittoral clean gravel or coarse sand	Substratum loss Smothering Change in suspended sediment Desiccation Change in emergence regime Change in salinity Change in oxygenation Abrasion & physical disturbance Extraction	
Zostera marina / angustifolia beds in lower shore or infralittoral clean or muddy sand	Substratum loss Smothering Change in turbidity Change in wave exposure Change in nutrient levels Introduction of microbial pathogens / parasites	
Ostrea edulis beds on shallow sublittoral muddy sediment	Substratum loss Smothering Increase in wave exposure Synthetic compound contamination Introduction of microbial pathogens / parasites Introduction of non-native species Extraction	
Serpula vermicularis reefs on very sheltered circalittoral muddy sand	Substratum loss Increase in water flow rate Increase in wave exposure Displacement Increase in salinity	
Brissopsis lyrifera and *Amphiura chiajei* in circalittoral mud	Increase in wave exposure	
Styela gelatinosa and other solitary ascidians on very sheltered deep circalittoral muddy sediment	Increase in temperature	

10 Some questions addressed

10.1 Can species diversity help resistance to change?

The mixture of producers, consumers and scavengers including key structural or functional species in a community determines the character of the community. If a key functional species is entirely lost (for instance sea urchins, as a result of disease), the character of the community will change drastically and it will become another, perhaps less valued, community. If however, one of many grazing species is lost, the remaining species may compensate for the loss and there will be little visible change – resistance to change is high. The large number of grazing species in the community provides ‘redundancy’.

The theory is similar for structural species. Some structural species are very important and, if that single species is destroyed, the associated community will collapse. For instance, horse mussel beds, *Serpula vermicularis* reefs, maerl beds, file shell *Limaria hians* reefs, sea grass beds.

However, the functional consequences of species loss do not always allow for ‘redundant’ species to compensate for the loss. Solan and others (2004) used models to predict how local extinctions would affect bioturbation in benthic invertebrate communities in Galway Bay. This study showed that when a species’ risk of extinction co-varied with body size or abundance, the compensatory responses did not alter the consequences of loss. This was because larger species, and those with lower abundances, were assumed to be more at risk of extinction. As a result, the loss of larger species or larger populations would have had a greater impact on bioturbatory function that the remaining species may not have been able to compensate for.

10.2 What makes a non-native species ‘invasive’?

Of the 60 or so non-native species that have established in the seas around the UK, a minority have had a harmful effect in displacing native species including changing habitats so significantly that the community changes (see 5.3). The reasons that a non native species may become invasive include:

1. it is able to dominate a vacant niche;
2. there is an ‘ideal’ habitat available;
3. there is sufficient suitable food;
4. there are no or few or ineffective native predators, and
5. it has aggressive chemical defences.

10.3 Is there a ‘canary in the coal mine’? – signals and indicators of change and quality

‘Quality’ is extremely difficult to define and whether or not the marine communities at a location are achieving their quality potential or might be ‘degraded’ needs much personal experience as well as data analysis. Work is currently underway to identify quality measures for application of the Water Framework Directive where quality status classes are:

1. **High Quality.** The composition of animal taxa is consistent with undisturbed conditions and disturbance sensitive taxa are present. There are no disturbance – favoured species found and no non-native species.
2. **Good Quality**. The composition of animal taxa is consistent with undisturbed conditions although species diversity (as number of species) may be below expected. Most of the disturbance sensitive taxa are present and/or there are some disturbance-favoured taxa present and/or non-native species.
3. **Moderate Quality.** The composition of animal taxa is predominantly consistent with undisturbed conditions although species diversity (as number of species) may be below expected and/or disturbance-sensitive taxa are absent and/or significant numbers of the disturbance-favoured taxa are present and/or non-native species dominate in places.
4. **Poor Quality.** Taxonomic diversity is low. The hard substratum is dominated by disturbance-favoured taxa and disturbance sensitive taxa are absent and/or the hard substratum is dominated by non-native species.
5. **Bad Quality.** Taxonomic diversity is very low. The hard substratum is occupied only by disturbance - highly favoured or neutral taxa.

It has proved possible to develop a sediment biology tool as there are many studies that have investigated impacts of effluents and contaminants or other stressors on sediment species. Pearson & Rosenberg (1978), for example, studied succession in macrobenthic communities in relation to organic enrichment (Figure 26).

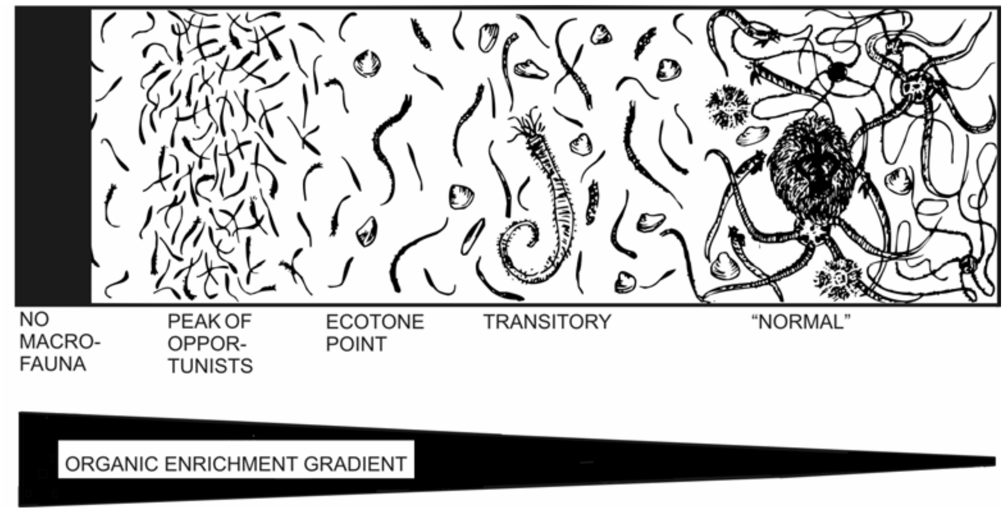


Figure 26 Diagrammatic representation of changes in abundance and species types along a generalised organic enrichment gradient. From: Pearson & Rosenberg, 1978.

With regards to hard substratum, Hoare & Hiscock (1974) studied the effects that the effluent of a bromine extraction plant had on a rocky shore community (illustrated in Figure 27).

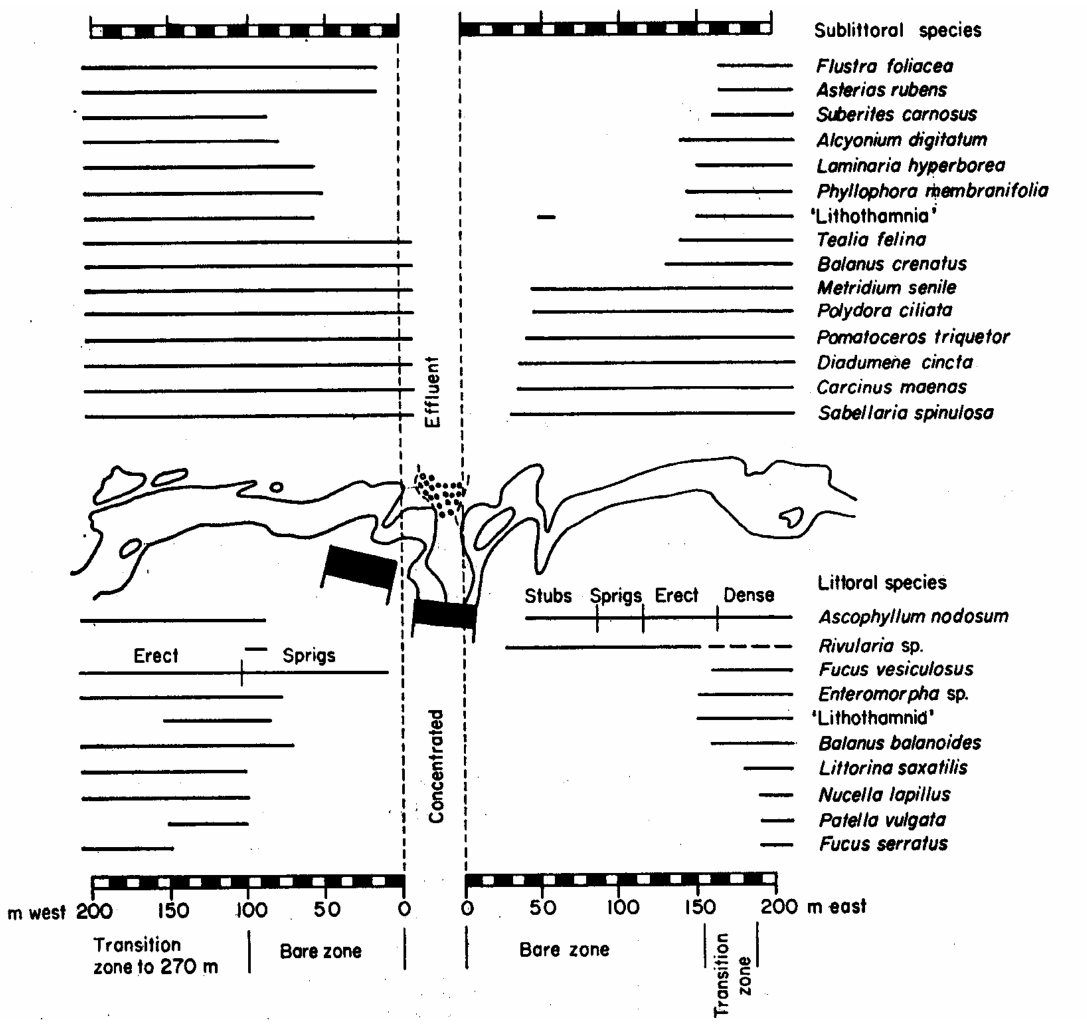


Figure 27 Distribution of conspicuous intertidal and subtidal species for a distance 200 m west and east of an acidified halogenated effluent. The coastline is depicted horizontally in the middle of the drawing. One of the few studies that identifies hard substratum species intolerant of or favoured by a human factor. From: Hoare & Hiscock, 1974.

Species or physical and chemical measures that give early warning of change occurring and of the quality of habitats in a location are known as '**indicator species**' and they help to represent what changes are happening in an otherwise complex ecosystem (Plates 27 to 33). Species that are 'intolerant of' or 'favoured by' changes have been identified through a wide variety of observational or experimental studies and are summarised in Hiscock and others (2005) and can be accessed through http://www.marlin.ac.uk/indicatorspp.

The International Council for the Exploration of the Seas (ICES) has, perhaps, the longest history of working to identify benthic indicator species. Their work is now closely linked to OSPAR. The ICES Advisory Committee on Ecosystems (http://www.ices.dk/iceswork/ace.asp) has recommended properties of good indicators (from political to scientific) of environmental quality:

- Relatively easy to understand by non-scientists and those who will decide on their use.
- Sensitive to a manageable human activity.

- Relatively tightly linked in space and time to that activity.
- Easily and accurately measured, with a low error rate.
- Responsive primarily to human activity, with low responsiveness to other causes of change.
- Measurable over a large proportion of the area in which the indicator is likely to be used.

Based on an existing body of time-series of data to allow a realistic setting of objectives.

Plate 27 Red seaweeds are sensitive to contaminants. Here, kelp plants distant from a factory producing halogenated acidified effluent (Site D) are colonised by algae whereas the kelp plants offshore of the effluent (Site E) are not. Image Keith Hiscock.

Plate 28 In instances where sediments become de-oxygenated, for instance due to organic enrichment below fish farms, the bacterium *Beggiatoa* grows. Image Keith Hiscock**.**

Plate 29 Native oysters thrive in areas where waters are clean of contaminants and free of disease. Image Keith Hiscock.

Plate 30 The burrowing brittle star *Amphiura filiformis* is adversely affected by hydrocarbons. Monitoring increases or reductions in the area where the brittle star is abundant shows whether pollution effects are increasing or decreasing. Image Keith Hiscock.

Plate 31 Ross worm *Sabellaria spinulosa* is characteristic of areas where suspended sediment levels are high and/or pollution/disturbance favours fast growing and short-lived species. Image Keith Hiscock.

Plate 32 *Polydora ciliata* tube worms live in chalk or limestone rock and are abundant in clean conditions. They also thrive in polluted conditions. Image Keith Hiscock.

Plate 33 Basking sharks do not make good indicators of quality or change as numbers can only be recorded when, where and if they come near the surface to feed. Image: John Boyle.

The properties of a good indictor listed by ICES are difficult to achieve and there are few species that fit the criteria and can be used in a meaningful way. An exception occurred with the use of tributyl tin (TBT) antifouling paint. The use of TBT brought about one of the greatest ‘disasters’ to hit marine life, at least in enclosed areas of coast (see eg Bryan and others 1986). Possible ‘signals’ (indicators) that the ecosystem was suffering in some way (for instance, the lack of late stage oyster larvae in the plankton, and imposex and localised extinction of the dog whelk) were not spotted and only when severe impacts such as shell thickening in oysters occurred were investigations commenced. What scientists failed to realize was that TBT was having a widespread and disastrous impact on benthic biodiversity with a large number of species adversely affected, especially at their larval stage (Figure 28). In the upper Crouch estuary, over the ten years following the banning of use of TBT on small vessels, the number of seabed species present there doubled (Rees and others 2001).

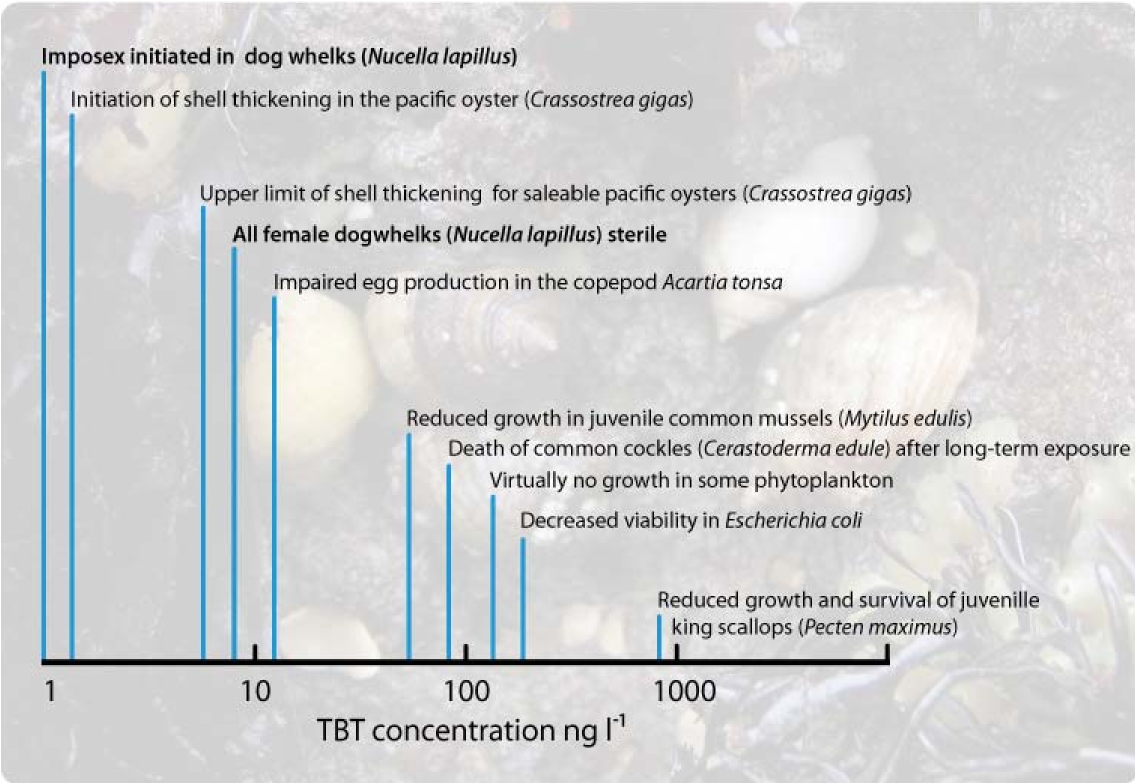


Figure 28 Sensitivity to tributyl tin contamination (ng l^{-1}) of various marine organisms. The responses range from subtle effects on individuals to acute effects on species populations. From: Hawkins and others 1994 and based on several studies.

11 Practical use of all of the above

BOX 7

Shifting from managing by sectoral activities and 'special' features to one focussed on ecosystem structure, functioning and processes – a viewpoint

Identifying the likely effects of human activities and natural events together on marine ecosystems requires a better understanding of how those different activities and events interact. What is clear is that some activities and natural events are overwhelmingly important in their potential to change the properties of those ecosystems and the structure and functioning of the communities that live there.

Most ecosystems can be 'tough' – they have resistance and resilience in the face of both natural and human-induced change. That resistance and resilience comes in part from the diversity of organisms in the systems and the possibilities of structural and functional species redundancy.

However, some human activities weaken the structural and functional foundations that help maintain biodiversity, the consequent built-in redundancy, and therefore resistance to change.

Furthermore, some human activities completely change habitats so that what was there in the way of species and communities is changed. That change can be catastrophic and irreversible, and matters very much if it adversely affects environmental goods and services and important features of biodiversity.

There is also a danger, in emphasising the 'ecosystem approach' of ignoring localised features such as the presence of nationally important species or biotopes which, whilst not obviously contributing to structure and functioning, are a valued part of our natural heritage.

Environmentally damaging activities are often very obvious but politically inconvenient to take action to prevent. Whilst having a good understanding of marine ecology is important for policy advisors, trying to make decisions about environmental protection and management based on understanding "ecosystem structure, functioning and processes" may be a displacement activity that results in us losing precious parts of our biodiversity as a result of obviously damaging activities while our attention is elsewhere.

Keith Hiscock
28 July 2007

11.1 Introduction

The summary of ecosystem structure and ecological processes shaping functioning presented here is aimed at informing decision makers who manage human activities in the marine environment to ensure its sustainable use and preservation. Combined with information on the distribution, sensitivity and importance of particular biotopes and species, the above should help to understand why some communities and locations are richer in species than others and what will happen in relation to various human activities.

11.2 High biodiversity recipe

There are many reasons why high species richness might develop at a location. Table 4 lists and explains some of them (including some overlapping ones).

Table 4 Factors contributing to high biodiversity at a given area.

	Explanation
Physical and chemical properties	
Strength of water movement	In general, the number of species that can survive in extremely wave exposed conditions (for instance a surge gully) or extremely wave sheltered conditions (for instance a flooded quarry) is much less than will survive in intermediate conditions. The situation is similar for tidal flow, although the communities that result in extremely strong and weak flow situations are different to those related to wave exposure. **Overall, the richest communities appear to be in situations where moderate water flow brings plentiful food for suspension feeders but is not destructive.**
Salinity	Marine organisms mostly require a salinity of more than 30 to survive and thrive. In variable or low salinity conditions, the variety of species will be reduced. **Therefore, highest species richness is likely to be in full salinity conditions.**

	Explanation
Physical and chemical properties	
Temperature	**As a general rule, the number of species is higher in warmer waters of the UK.** Mediterranean-Atlantic species outnumber arctic-boreal species. The movement of warmer water along the western seaboard of the British Isles is important and high species richness can occur further north than might be expected.
Disturbance regime	**High species richness may be found in disturbed situations (particularly hard substrata) and in undisturbed situations (particularly soft substrata)**. The 'Intermediate Disturbance Hypothesis' (see Connell 1978 for a marine perspective) is a mechanism for species co-existence based on patch dynamics in which catastrophic events create empty patches before one species has the chance to exterminate weaker competitors. The 'Stability-time hypothesis' (Sanderson, 1969) suggests that, in environmentally stable situations where space in the community is not dominated by a few competitively superior species and where predators are not in high abundance, species richness may be high because of that stability. The longer that a habitat remains undisturbed by extreme environmental conditions, the more species will settle and survive, including low abundance species, many of which may only recruit infrequently but live for a long time.
Large-scale physical processes	
Residual water currents	Water currents determine the distribution of water bodies of particular characteristics and therefore 'water quality' in its broadest sense. They also carry propagules of species and, if their direction is away from a location, that location may not receive propagules. Examples would include offshore islands where a combination of unfavourable currents and short life of planktonic larvae would lead to an impoverished biota. **Where a location is close to and 'downstream' of rich communities, species richness is likely to be high.**
Structural or functional attributes	
Architectural diversity	Organisms have niche preferences – for aspect, shade, open/crevice etc. **Therefore, a hard substratum habitat with a high architectural diversity should attract a high variety of species.**
Geological diversity	Particular organisms may need different 'hardness' of substrata. Soft substrata provide opportunities for boring species not available on hard substrata.
Hydrodynamic diversity	Architectural features create a barrier to flow with some parts of the substratum where accelerated flow occurs (desirable for a passive suspension feeder) and some areas where flow is reduced (desirable for weakly attached species such as some sea anemones).
Shelter from predators	Shelter takes many forms – it can be in the haptera of a kelp holdfast, deep in a crevice, hidden from view under an algal canopy or in a burrow in the seabed.

	Explanation
Physical and chemical properties	
Facilitation	Some organisms need the presence of a host or an action or an incidental effect of another species being present. For instance: corals provide a favoured (the only) substratum that the barnacle *Bostrichia anglicum* lives on (Plate 8); some algae and animals only settle on a particular other species, for instance the tube worm *Spirorbis borealis* on bladder wrack *Fucus vesiculosus*; grazing by urchins clears spaces, prevents a few species becoming dominant and makes available settlement opportunities; filtering of suspended particles by shellfish, ascidians etc. may create clearer water enabling greater downward penetration of algae and sea grasses. Some species, by their presence, stabilize sediment and prevent outwash, for instance, the sand mason worm *Lanice conchilega*, sea grass *Zostera marina*, ross worm *Sabellaria spinulosa.*
Complementary food sources	Some animals feed from the plankton, some are hunters, others wait for food to pass by or fall from above, some feed from the benthos, some take suspended particulate matter, some take deposited particulate matter etc.
Complementary use of nutrients	Some plants utilize ammonia, some nitrates
Complementary use of light spectra	Particularly in the plankton, species that exploit different parts of the light spectra are likely to thrive at different depths and, whilst competing for nutrients, they are not competing for light.

11.3 Questions about the establishment and management of mpas

Management question	Structure, function and process questions to answer
Where should I set the boundary?	Where are the main features (physical and biological) for which the site is established and how far away do species forage? Where do the main sources of food and nutrients come from and can they be within the boundary?
Which species really matter to protect?	Which species are long-lived, slow-growing and have benthic larvae? Which species are key structural or functional species (ecosystem engineers)?
Which species will look after themselves or nothing can be done to protect them?	Which species settle frequently or from distant sources and are fast growing?

11.4 What will happen if ……? questions

Management question	Structure, function and process questions to answer
If the population of species ‘a’ is killed, will it return?	Where is the nearest surviving population and is it near enough for migration or propagule dispersal of the species to occur to the location?
Will it ‘matter’ to Biodiversity Action Plan species ‘b’ if seawater temperature rises?	Will species ‘b’ thrive/decline because of temperature (in)tolerance including effects on reproduction? Will facilitating species be adversely affected (ie they are lost because of temperature intolerance)?

If predator 'c' is removed, how will the community be affected?	Does predator 'c' play a key structural or functional role within the community? What are predator 'c''s prey species and will a reduction in the abundance of predator 'c' result in an increase in prey abundance? If so, what effects will this have on species lower down the food web? Does anything feed on predator 'c' and if so, is there an alternative food source?
If predator 'd' increases in abundance, how will it affect the community.	What are predator 'd''s prey species and will an increase in the abundance of predator d have a negative impact on the prey? If so, what effect will this have on the rest of the food web? Are there any predators of predator d that may benefit from an increase in its abundance?
Physical disturbance homogenises structural complexity.	There will be fewer niches available for species to shelter and for species with preferences for different orientations of substrata to settle. Overall, a decline in species richness including possibly loss of food species and species of natural heritage value. If the loss of species reduces resilience, the system may become pre-disposed to sudden and dramatic change.
If I block water flow in tidal narrows, what will happen to the marine life?	Are any community assemblages downstream from the tidal narrows that rely on the fast water flow for food, spawning etc?
If the level of silt increases in biotope, what will happen?	How long is the increase in level of silt likely to persist? Are there any species within the biotope that are highly sensitive to increased silt levels?
How long will it take a community of species to re-establish after dredging?	Is the habitat in a state suitable for recolonization? Where are the nearest surviving populations of species represented within the community and are they near enough for migration or propagule dispersal of the species to occur to the location? What are the recovery characteristics of species within that community and how long is the process likely to take?

11.5 A 'worksheet' to identify ecosystem needs

The dossiers in the Appendix are examples of completed worksheets. The worksheet approach could be used as a management tool when developing management plans for areas.

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13 Glossary

Alien species. A non-established introduced species (q.v.), which is incapable of establishing self-sustaining or self-propagating populations in the new area without human interference (cf. 'introduced species'; 'non-native').

Anaerobic. An environment in which the partial pressure of oxygen is significantly below normal atmospheric levels; deoxygenated (Lincoln and others 1998).

Anoxic. Devoid of oxygen.

Assemblage. A generic term used chiefly by some British marine ecologists which does not assume interdependence within a community or association, but appears to have the same broad definition as 'community' (based on Hiscock & Connor, 1991).

Benthos. Those organisms attached to, or living on, in or near, the seabed, including that part which is exposed by tides as the littoral zone (based on Lincoln & Boxshall, 1987).

Biodiversity. "The variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems." (UN Convention on Biological Diversity, 1992).

Biomass. The total quantity of living organisms in a given area, expressed in terms of living or dry weight or energy value per unit area.

Biotope. 1) The physical 'habitat' with its biological 'community'; a term which refers to the combination of physical environment (habitat) and its distinctive assemblage of conspicuous species. MNCR uses the biotope concept to enable description and comparison. 2) The smallest geographical unit of the biosphere or of a habitat that can be delimited by convenient boundaries and is characterized by its biota (Lincoln and others 1998).

Bioturbation. The mixing of a sediment by the burrowing, feeding or other activity of living organisms (Lincoln and others 1998).

Boxcosm. A container where environmental conditions can be experimentally manipulated.

Calanoid. A free-living and largely planktonic order of copepods with very long first antennae. Includes *Calanus* spp. (Barnes, 1987).

Circalittoral. The subzone of the rocky sublittoral below that dominated by algae (the infralittoral), and dominated by animals. No lower limit is defined, but species composition changes below about 40 m to 80 m depth, depending on depth of the seasonal thermocline. This subzone can be subdivided into the upper circalittoral where foliose algae are present and the lower circalittoral where they are not (see Hiscock, 1985). The term is also used by Glémarec (1973) to refer to two étages of the sediment benthos below the infralittoral: a "coastal circalittoral category with a eurythermal environment of weak seasonal amplitude (less than 10°C) varying slowly" and a "circalittoral category of the open sea with a stenothermal environment".
1) lower The part of the circalittoral subzone on hard substrata below the maximum depth limit of foliose algae (based on Hiscock, 1985).
2) upper The part of the circalittoral subzone on hard substrata distinguished by the presence of scattered foliose algae amongst the dominating animals; its lower limit is the maximum limit of depth for foliose algae (based on Hiscock, 1985).

Classification. 1) taxonomy - the placing of animals and plants in a series of increasingly specialized groups because of similarities in structure, origins etc., that indicate a common relationship (from Makins, 1991). 2) biotopes - the process of identifying distinctive and recurrent groupings of species with their associated habitat and describing them within a structured framework.

Community. A group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and identifiable by means of ecological survey from other groups (from Mills, 1969; see Hiscock & Connor, 1991 for discussion).

Conservation. "The regulation of human use of the global ecosystem to sustain its diversity of content indefinitely" (Nature Conservancy Council, 1984).

Constancy. 1) The frequency of occurrence of a species in samples from the same community (based on Makins, 1991). 2) The continued presence of a species or community at a particular location. (Cf. 'persistence', 'resilience', 'stability').

Copepod. A subclass of crustacea. Mostly small (a few mm long) with no compound eyes or carapace (Eleftheriou, 1997). Over 7,500 species have been described and marine copepods are usually the most abundant and conspicuous component of a plankton sample (Barnes, 1987).

Demersal. Living at or near the bottom of a sea or lake, but having the capacity for active swimming (from Lincoln and others 1998).

Deposit feeders. Any organisms which feed on fragmented particulate organic matter in or on the substratum; detritivores (from Lincoln and others 1998).

Diel. Daily, pertaining to a 24 hour period (Lincoln and others 1998).

Dinoflagellate. (from Thain & Hickman, 1994).Important unicellular freshwater and marine planktonic algae. Dinoflagellates proper are motile and are biflagellated. The transverse flagella causes forward motion and the longitudinal flagellum acts as a rudder. Some species are bioluminescent. Some produce toxins which result in the death of fish and shellfish as part of ‘red tides’. Humans may also die as a result of eating contaminated shellfish

Disturbance. "A chemical or physical process caused by humans that may or may not lead to a response in a biological system within an organism or at the level of whole organisms or assemblages. Disturbance includes stresses". (from Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection - GESAMP, 1995).

Diversity. The state or quality of being different or varied (from Makins, 1991).
1) In relation to species, the degree to which the total number of individual organisms in a given ecosystem, area, community or trophic level is divided evenly over different species, ie measure of heterogeneity. Species diversity can be expressed by diversity indices, most of which take account of both the number of species and number of individuals per species (Based on Baretta-Bekker and others 1992). Cf. 'evenness'; 'richness'.
2) In conservation assessment - an assessment of the richness of different types in a location (which can be large or small) including the number of different biotopes and numbers of species. The number of species present in an example of a particular biotope.

Ecosystem. A community of organisms and their physical environment interacting as an ecological unit (from Lincoln and others 1998). Usage can include reference to large units such as the North Sea down to much smaller units such as kelp holdfasts as "an ecosystem".

Environment. The complex of biotic climatic, edaphic and other conditions which comprise the immediate habitat of an organism; the physical, chemical and biological surroundings of an organism at any given time. (cf. 'habitat') (from Lincoln and others 1998).

Epibenthic. Living on the surface of the seabed.

Epiphytic. Growing on the surface of a living plant (but not parasitic upon it).

Euphausid. A taxonomic subgroup of crustaceans which includes shrimp and krill.

Eutrophication. The over-enrichment of an aquatic environment with inorganic nutrients, especially nitrates and phosphates, often anthropogenic (eg sewage, fertilizer run-off), which may result in stimulation of growth of algae and bacteria, and can reduce the oxygen content of the water.

Evenness. This is a measure of equitability: a measure of how evenly individuals are distributed among the different species (Clarke & Warwick, 2001).

Fecundity. The potential reproductive capacity of an organism or population, measured by the number of gametes (eggs) or asexual propagules.

Filter feeder (see suspension feeder)

Fission. Form of asexual multiplication involving division of the body into two or more parts each or all of which can grow into new individuals (Barnes and others 1993).

Functioning. The mode of action by which the system fulfils its purpose or role, as determined by its component elements. In terms of ecosystem functioning; the activities, processes or properties of ecosystems that are influences by its biota (Naeem and others 2004).

Gonochoristic. Having separate sexes (cf. 'hermaphroditic') (Barnes and others 1993).

Grazers. 1) Animals which: rasp benthic algae (or sessile animals, such as bryozoan crusts) from the substratum, or 2) animals which ingest phytoplankton from the water column by suspension-feeding (q.v.).

Habitat. The place in which a plant or animal lives. It is defined for the marine environment according to geographical location, physiographic features and the physical and chemical environment (including salinity, wave exposure, strength of tidal streams, geology, biological zone, substratum, 'features' (eg crevices, overhangs, rockpools) and 'modifiers' (eg sand-scour, wave-surge, substratum mobility). (Cf. 'environment').

Heavy metal. A generic term for a range of metals with a moderate to high atomic weight, for example cadmium, mercury, lead. Although many are essential for life in trace quantities, in elevated concentrations most are toxic and bioaccumulate, and so are important pollutants.

Herbivores. Organisms which feed on plants, including phytoplankton.

Hermaphroditic. Capable of producing both ova and spermatozoa either at the same time (permanent) or sequentially (cf. protandry, protogyny, gonochoristic) (Barnes and others 1993).

Imposex. An abnormality of the reproductive system in female gastropod molluscs, by which male characteristics are superimposed onto female individuals (Smith, 1980), resulting in sterility or, in extreme cases, death. This may be caused by hormonal change in response to pollution from organotin antifoulants, even at low concentrations. See 'organotin'.

Infauna. Benthic animals which live within the seabed.

Infralittoral. A subzone of the sublittoral in which upward-facing rocks are dominated by erect algae, typically kelps; it can be further subdivided into the upper and lower infralittoral (based on Hiscock, 1985). The term is also used by Glémarec (1973) to refer to areas (étages) with a eurythermal environment of great seasonal and also daily and tidal amplitude. 1) lower The part of the infralittoral subzone which, on hard substrata, supports scattered kelp plants (a kelp park) or from which kelps are absent altogether and the seabed is dominated by foliose red and brown algae. It may be difficult to distinguish the lower infralittoral where grazing pressure prevents the establishment of foliose algae.
2) upper The part of the infralittoral subzone which, on hard substrata, is dominated by Laminariales forming a dense canopy, or kelp forest (based on Hiscock, 1985).

Intertidal. The zone between the highest and lowest tides (from Lincoln and others 1998).

Introduced species. Any species which has been introduced directly or indirectly by human agency (deliberate or otherwise), to an area where it has not occurred in historical times and which is separate from and lies outside the area where natural range extension could be expected (ie outside its natural geographical range (q.v.)). The term includes non-established introductions ('aliens' (q.v.)) and established non-natives (q.v.), but excludes hybrid taxa derived from introductions ('derivatives').

Kelp forest. A belt of the upper infralittoral (q.v.) subzone on hard substrata, dominated by Laminariales sufficiently dense to form an almost continuous canopy.

Littoral. The area of the shore that is occupied by marine organisms which are adapted to or need alternating exposure to air and wetting by submersion, splash or spray. On rocky shores, the upper limit is marked by the top of the *Littorina* /*Verrucaria* belt and the lower limit by the top of the laminarian zone (Lewis, 1964). It is divided into separate subzones, particularly marked on hard substrata. Cf. 'intertidal'.

Maerl. Twig-like unattached (free-living) calcareous red algae, often a mixture of species and including species which form a spiky cover on loose small stones - 'hedgehog stones'.

Mesocosm. Tanks where environmental conditions can be manipulated.

Nauplii (sing. nauplius). First (earlier) of two basic stages in the larval development of copepods (based on Stachowitsch, 1992).

Non-native (species) A species which has been introduced directly or indirectly by human agency (deliberate or otherwise), to an area where it has not occurred in recent times (about 5,000 years BP) and which is separate from and lies outside the area where natural range extension could be expected (ie outside its natural geographical range (q.v.)). The species has become established in the wild and has self-maintaining populations; the term also includes hybrid taxa derived from such introductions ('derivatives'). (Cf. 'alien species'; 'introduced species'; 'recent colonist'; 'reintroduction').

North Atlantic Oscillation (NAO). The difference in pressure at sea level between the Azores and Iceland during the winter (www.sahfos.ac.uk). The NAO is associated with winter fluctuations in temperatures, rainfall and storminess over much of Europe. When the NAO is 'positive', westerly winds are stronger or more persistent, northern Europe tends to be warmer and wetter than average and southern Europe colder and drier (www.metoffice.com).

Parasite. An organism that lives in or on another living organism (the host), from which it obtains food and other requirements. The host does not benefit from the association and is usually harmed by it. (cf. commensalism, mutualism, symbiosis).

Pelagic zone. The open sea and ocean, excluding the sea bottom. Pelagic organisms inhabit such open waters.

Persistence. The continued presence of species or communities at a location (usually inferring in spite of disturbance or change in conditions) (cf. 'constancy', 'stability', 'resilience').

Photosynthesis. The biochemical process that utilizes radiant energy from sunlight to synthesize carbohydrates from carbon dioxide and water in the presence of chlorophyll and other photopigments (based on Lincoln and others 1998).

Phytoplankton. Planktonic plant life: typically comprising suspended or motile microscopic algal cells such as diatoms, dinoflagellates and desmids (based on Lincoln & Boxshall, 1987).

Propagule. Any part of an organism, produced sexually or asexually, that is capable of giving rise to a new individual (from Lincoln and others 1998).

Protandrous . A condition of hermaphroditism in plants and animals where male gametes mature and are shed before female gametes mature (Holmes, 1979).

Protogyny. A condition of hermaphroditism in an organism that assumes a functional female condition first during development before changing to a functional male state (Lincoln and others 1998).

Recent colonist. A species which, without any human intervention, has extended its natural geographical range (q.v.) in recent times and which has established new self-maintaining and self-regenerating populations in the wild (cf. 'non-native'; 'vagrant').

Regime shift. A sustained change in the production characteristics of an ecosystem and its components.

Reintroduction. A species which has been reintroduced by human agency, deliberate or otherwise, to an area within its natural geographical range (q.v.) but where it had became extinct in historical times.

Resident. A permanent inhabitant, non-migratory.

Resilience. The ability of an ecosystem to return to its original state after being disturbed (from Makins, 1991) (cf. 'constancy', 'persistence', 'stability').

Richness (species). The number of species in a community, habitat or sample (cf. 'diversity'; 'evenness').

Salinity. A measure of the concentration of dissolved salts in seawater. Salinity is defined as the ratio of the mass of dissolved material in sea water to the mass of sea water (UNESCO, 1985). But this 'absolute' definition is not practical. Salinity was measured by a chlorinity titration but with the development of the salinometer, which utilizes conductivity, a new definition was developed. The 'practical salinity' (S) of a sea water sample is defined as the ratio of the electrical conductivity of the sample (at 15 °C, and one standard atmospheric pressure) to that of a standard solution of potassium Chloride (KCl). A ratio of 1 is equivalent to a 'practical salinity' of 35 (UNESCO, 1985). Until recently, salinity was expressed as parts per thousand (ppt or ‰). Subsequently, adoption of the 'practical salinity' gave rise to the 'practical salinity unit' (psu). However 'salinity', defined as the ratio of two quantities of the same unit, is a 'dimensionless quality', ie takes no units. Therefore, it is correct to speak of a salinity of 35 (UNESCO, 1985). Baretta-Bekker and others (1992) suggested that, in most cases, where a high degree of accuracy is not required, old and new figures for salinity can be used interchangeably. However for the sake of accuracy, when referring to salinity in our on-line reviews, the units used by the original authors are quoted in the text. Freshwater is regarded as < 0.5 ‰ (limnetic), seawater as > 30 ‰ (euhaline), and brackish water as intermediate, including oligohaline, mesohaline and polyhaline waters (based on McLusky, 1993).

Scavenger. Any organism that feeds on dead organic material.

Silt. Fine-grained sediment particles ranging in size from 0.004 mm to 0.0625 mm (based on Wentworth, 1922).

Stability. The ability of an ecosystem to resist change (from Makins, 1991) (cf. 'constancy', 'persistence', 'resilience').

Stratification The division of a water body into layers of different temperature and density, owing to the development of a thermocline (Eleftheriou, 1997). Stratification may also occur as a result of the development of a halocline (division of areas of high and low salinity water). The stratification prevents mixing between the different water layers.

Structure. The combination of mutually connected and dependant biological and non-biological elements of a system that determine its nature.

Sublittoral. The zone exposed to air only at its upper limit by the lowest spring tides, although almost continuous wave action on extremely exposed coasts may extend the upper limit high into the intertidal region. The sublittoral extends from the upper limit of the large kelps and includes, for practical purposes in nearshore areas, all depths below the littoral. Various subzones are recognised (based on Hiscock, 1985.)

Suspension feeders. Suspensivores, filter-feeders, any organisms which feed on particulate organic matter, including plankton, suspended in the water column (from Lincoln and others 1998).

Vagrant. Individuals of a species which, by natural means, move from one geographical region to another outside their usual range, or away from usual migratory routes, and which do not establish a self-maintaining, self-regenerating population in the new region (cf. 'alien species'; 'recent colonist').

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Appendix: Dossiers

Structure & functioning – characterization and importance for management habitat: Intertidal mud flats

Severn Estuary mudflats. Image: Kathryn Birch/CCW.

Mudflats that include gravel may be particularly rich in species. Tosnos Point, Salcombe Harbour. Image: Keith Hiscock.

Key: Very High ✓✓✓✓, High ✓✓✓ , Low ✓✓, Very Low ✓ Not Relevant NR, Not possible to manage NP

	Importance to biological community	Likelihood of change	Management priority
Physical & chemical properties & processes			
Wave action	✓✓✓✓	✓	NP*
Tidal flow strength	✓✓✓	✓	NP*
Immersion / emersion	✓✓✓✓	✓	NP*
Salinity	✓✓✓✓	✓	NP*
Supply of nutrients	✓✓✓✓	✓✓✓	✓✓✓
Supply of oxygen to the sediment (both through bioturbation / burrows and the availability of oxygen in the water column)	✓✓✓✓	✓✓✓	✓✓✓
Availability of suitable substratum	✓✓✓✓	✓✓	✓
Light	✓✓✓	✓✓	✓✓
Contaminants	✓✓✓	✓✓✓	✓✓✓
Sedimentation	✓✓✓	✓✓✓	✓✓✓
Structure	✓✓✓✓		
Physical (sediment size, degree of sorting)	✓✓✓✓	✓✓	✓✓
Biological (burrows, casts)	✓✓✓✓	✓✓	✓✓
Biological - the presence / absence of particular species	✓✓✓	✓✓	✓✓
Functioning (as processes)			
Food supply remote (suspended particles, detritus, dissolved organic matter)	✓✓✓✓	✓✓	✓✓
Food supply local (predation, deposit feeding)	✓✓✓✓	✓✓	✓✓
Primary productivity	✓✓✓	✓✓	✓✓
Connectivity (larval dispersal & recruitment)	✓✓✓	✓✓	✓✓

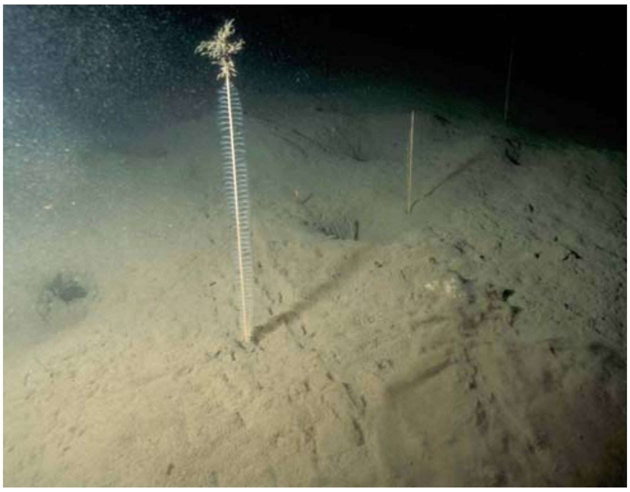
- Intertidal mudflats are heavily influenced by biological, chemical *and* physical processes including predation, nutrient cycling and tidal movement respectively.

- Many processes in and on the mudflats are strictly influenced by the state of the tide. For example, predation by fish will occur at high tide whilst predation by birds will occur at low tide.
- Much of the infauna are deposit feeders, taking advantage of the high levels of organic material in the sediment. Organic material is degraded by microorganisms and recycled.
- Due to high organic content of muds (which results in the presence of large microbial populations that use lots of oxygen) and the small and compact nature of the sediment particles, oxygen within the sediment is limited. The sediment profile can crudely be divided into an overlying oxygenated later at the top and a black anoxic layer underneath. This affects the distribution of infauna since many are restricted to the oxygenated layer although others penetrate deeper in irrigated burrows or extend their burrows upwards into the oxygenated layer there is a high oxygen demand within the sediment.
- Unlike rocky shores, which may experience huge fluctuations in salinity, pH and temperature over the course of the tidal cycle, the sediment in mudflats act as a buffer against these large changes and provide a relatively stable environment for the associated flora and fauna. The sediment is often relatively highly stable too, although the top layers may get removed depending on the height of the tide / wave action, and on the level of cohesion within the sediment.
- The loss of intertidal mudflats due to habitat reclamation and colonization by saltmarsh plants such as *Spartina anglica*, has led to the loss of this vast feeding are for many important wading and over-wintering birds.
- Large macroalgae are rare and generally restricted to pebbles and rocks on the mudflat. Filamentous algal mats, especially *Ulva* sp., may be common in summer months, especially as a result of high nutrient levels which can result in the 'suffocation' of the habitat. Unicellular algae can produce brown or green films on the surface of the mud.

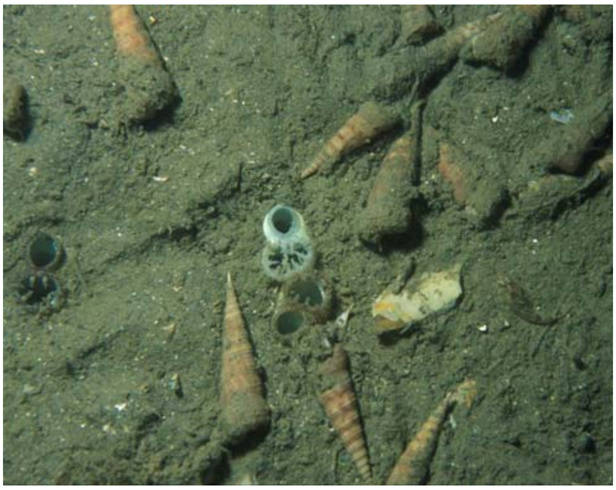
The most likely change in the character of intertidal mudflats will be as a result of chemical factors, such as eutrophication (excess nutrient loading), oil pollution or synthetic chemical contamination. Consented sewage discharges (commonplace in many estuaries) have the potential to cause large changes in the levels of ammonia, pH and suspended material in the water column. Because the water column and sediment are so intrinsically linked, this can have a direct impact on the mudflats. The effluent has a high Biological Oxygen Demand (BOD), meaning that the work involved breaking down all the organic material within it is such that the organisms responsible would use high amounts of oxygen in the process. As a result, there would be less oxygen the water column available for exchange with the sediment. Furthermore, metals such as mercury, cadmium and lead can be found within the effluent. These metals, and others, bind strongly with the suspended sediment in the effluent and settle out, introducing the contaminants to the mudflats.

NP* indicates that under normal conditions, these factors would not be manageable but, in extreme circumstance, such as the construction of tidal barrages, it is possible that they will change, leading to drastic and permanent changes in the community dynamics and functioning of the ecosystem.

Structure & functioning – characterization and importance for management habitat: Subtidal muds



Deep mud with sea pens (*Virgularia mirabilis*), a passive suspension feeder, and burrows of Norway lobster *Nephrops norvegicus*, a scavenger. Loch Duich. Image: Keith Hiscock.



The majority of mud community species are hidden from view, although feeding structures such as the siphons of the bivalve *Lutraria lutraria* may show. The turret shells are detritus feeders. Plymouth Sound. Image: Keith Hiscock.

Key: Very High ✓✓✓✓, High ✓✓✓ , Low ✓✓, Very Low ✓ Not Relevant NR, Not possible to manage NP

	Importance to biological community	Likelihood of change	Management priority
Physical & chemical properties & processes			
Wave action	✓✓	✓	NP
Tidal flow strength	✓✓✓	✓	NP
Immersion / emersion	NR	✓	NP
Salinity	✓✓✓✓	✓	✓
Supply of nutrients (through bioturbation)	✓✓✓✓	✓	✓
Supply of oxygen to the sediment (both through bioturbation / burrows and the availability of oxygen in the water column)	✓✓✓✓	✓	✓
Availability of suitable substratum	✓✓✓✓	✓	✓
Light	✓	✓	✓
Contaminants	✓✓✓	✓✓	✓✓
Sedimentation	✓✓✓	✓	✓
Structure			
Physical (sediment size, degree of sorting)	✓✓✓✓	✓✓	✓✓
Biological (burrows / casts)	✓✓✓✓	✓	✓
Biological - the presence / absence of particular species	✓✓✓✓	✓✓	✓✓

	Importance to biological community	**Likelihood of change**	**Management priority**
Functioning (as processes)			
Food supply remote (suspended organic matter, dissolved organic matter, detritus)	✓✓✓✓	✓	✓
Food supply local (predation, primary production where relevant)	✓✓✓✓	✓	✓
Primary productivity	✓✓	✓	✓
Connectivity (larval dispersal & recruitment)	✓✓✓	✓	✓

- Subtidal muds, due to their depth and the low-energy hydrographic regime, are very stable habitats and often highly diverse. The depth of water at which they are commonly found means that large or abrupt changes in properties such as temperature, salinity and the amount of suspended sediment are rare.
- Unlike intertidal mudflats, there is often a lower concentration of suspended inorganic material. As a result, the habitat is comparably more suitable for suspension feeders.
- Bioturbation is important for oxygenating the upper sediment layers, in addition to providing structural heterogeneity to the sediment.
- Due to high organic content of muds (which results in the presence of large microbial populations that use lots of oxygen) and the small and compact nature of the sediment particles, oxygen within the sediment is limited. The sediment profile can crudely be divided into an overlying oxygenated later at the top and a black anoxic layer underneath. This affects the distribution of infauna since many are restricted to the oxygenated layer although others penetrate deeper in irrigated burrows or extend their burrows upwards into the oxygenated layer there is a high oxygen demand within the sediment.
- Where sublittoral muds are shallow enough, benthic microalgae may be present although large macroalgae are rare. Microalgae is the only autochthonous source of organic material – allochthonous organic material comes from eg particulate organic material, sewage, detritus etc.

The most likely changes to subtidal muddy areas are likely to be physical, as a result of storms or bottom fishing / dredging. Of these, it is the fishing and dredging that is likely to cause the greatest change since these activities will result in the destabilization of the substratum. Trawling and dredging can result in the destruction of the complex burrow systems that are in part responsible for maintaining the biodiversity of the habitat and in the loss of some long-lived species such as some sea anemones.

Structure & functioning – characterization and importance for management habitat: Rocky shores

Grazing is an important factor in limiting abundance of algae on rocky shores. Ollaberry, Shetland. Image: Keith Hiscock.

Moderately exposed rocky shores with complex topography offer a wide range of habitats to plants and animals. Wembury Point. Image: Keith Hiscock.

Key: Very High ✓✓✓✓, High ✓✓✓, Low ✓✓, Very Low ✓ Not Relevant NR, Not possible to manage NP

	Importance to biological community	Likelihood of change	Management priority
Physical & chemical properties & processes			
Wave action	✓✓✓✓	✓	✓✓
Tidal flow strength	✓✓	✓	✓
Immersion / emersion	✓✓✓✓	✓	✓
Salinity	✓✓ (open shore) ✓✓✓ (localized)	✓ (open shore) ✓✓✓ (localized)	✓ (open shore) ✓✓✓ (localized)
Supply of nutrients	✓✓✓	✓✓	✓✓
Supply of oxygen (availability in the water column)	✓✓✓✓	✓✓	✓✓
Availability of suitable substrata	✓✓✓✓	✓✓	✓✓
Light	✓✓✓✓	NR	✓✓
Contaminants	✓✓✓	✓✓✓	✓✓✓
Sedimentation	✓✓✓✓	✓✓✓	✓✓✓
Structure			
Physical (rock hardness, degree of fissuring, presence of damp places eg under boulders)	✓✓✓✓	✓✓	✓✓
Biological (canopy shelter, turf refuge, holdfast refuge, attachment surfaces)	✓✓✓✓	✓✓✓✓	✓✓✓✓
Biological - the presence / absence of particular species	✓✓✓✓	✓✓✓✓	✓✓✓✓
Functioning (as processes)			
Food supply remote (suspension feeding)	✓✓	✓✓	✓✓
Food supply local (grazing, predation)	✓✓✓✓	✓✓✓✓	✓✓✓✓
Primary productivity	✓✓✓✓	✓✓	✓✓
Connectivity (larval dispersal & recruitment)	✓✓✓✓	✓	✓✓

- Rocky shore communities are dominated by physical factors (especially strength of wave action, degree of slope) and by biological interactions (domination of space, grazing and predation).
- Characterizing algae require light and nutrients. High nutrient levels (usually localized) may favour algal growth and result in the domination by green algae in places.
- Increased sediment loading can be detrimental to canopy species and may result in the domination by turf-forming algal species. The turf itself then traps sediment which becomes an important part of the turf structure.
- Many animals require localized food sources (obtained by grazing and predation) although barnacles and other suspension feeders feed from the water column.
- As a result of rainfall and evaporation, high fluctuations in salinity are a characteristic of shores but where freshwater lingers or dominates (upper shore pools, streams), green algae may dominate as grazers are displaced.
- Propagules (larvae/spores) of some rocky shore species (especially algae and some gastropod molluscs) may be distributed only a few kilometers, whilst others (for instance barnacles) may be capable of long-distance travel.

Rocky shore communities are likely to change in character if grazing species are lost (for instance after an oil spill) but recovery is rapid as life spans are relatively short (a few years) and recruitment occurs readily providing that similar unaffected shore types are nearby.

Structure & functioning – characterization and importance for management habitat: Subtidal photic rock

On the open coast, kelp plants dominate rocks to a depth equivalent to about where 10% of surface illumination is present. Garra Point. Image: Keith Hiscock.

In wave and tide exposed situations amenable to fauna, seaweeds may not be able to colonize despite sufficient light being present. Eddystone. Image: Keith Hiscock.

Key: Very High ✓✓✓✓, High ✓✓✓ , Low ✓✓, Very Low ✓ Not Relevant NR, Not possible to manage NP

	Importance to biological community	Likelihood of change	Management priority
Physical & chemical properties & processes			
Wave action	✓✓✓✓	NP	NP
Tidal flow strength	✓✓✓✓	NP	NP
Immersion / emersion	NR	NP	NP
Salinity	✓✓✓	NP	✓
Supply of nutrients	✓✓✓	✓✓	✓
Supply of oxygen (availability in the water column)	✓✓✓	NP	✓
Availability of suitable substrata	✓✓✓✓	✓✓	✓✓
Light	✓✓✓✓	✓	✓
Contaminants	✓✓	✓✓	✓✓
Sedimentation	✓✓	✓✓	✓✓
Structure			
Physical (rock hardness, degree of slope, presence of other sediment)	✓✓✓	✓	✓
Biological (canopy shelter, turf refuge, holdfast refuge, attachment surfaces)	✓✓✓✓	✓✓	✓✓
Biological - the presence / absence of particular species	✓✓✓✓	✓✓	✓✓
Functioning (as processes)			
Food supply remote (suspension feeding)	✓✓✓✓	✓✓	✓
Food supply local (grazing, predation)	✓✓✓✓	✓✓	✓
Primary productivity	✓✓✓	✓	✓
Connectivity (larval dispersal & recruitment)	✓✓✓	✓	✓

- There may be large differences in communities on vertical as opposed to gently sloping rock faces. There are several reasons for this including differences in light penetration, levels of sedimentation, predator mobility and the availability of different habitats such as boulders and cobbles.
- Light penetration decreases inversely with depth and an obvious algal zonation may be apparent, with shade tolerant red algae at lower depths where they are competitively superior to green and brown algae. The upper end of the photic zone may be dominated by luxuriant plant growth, especially kelps. At the lower end the algal community is likely to be more impoverished and dominated by encrusting red algae that are tolerant of intense sea urchin grazing.
- Intense competition may exist for space in some areas, resulting in a 'patchwork' of different species, as opposed to obvious banded zonation commonly attributed to many rocky shore communities.
- Many animals require localized food sources (obtained by grazing and predation) although barnacles and other suspension feeders feed from the water column. Vertical rocky communities may be dominated by suspension feeders since mobile predators may be restricted in terms of movement on vertical surfaces and particulate organic material, apart from where it gets trapped by various species and depending on water currents, is less likely to settle on the vertical surfaces to the detriment of grazers and detritivores.

Structure & functioning – characterization and importance for management habitat: Subtidal aphotic rock

Upward facing subtidal aphotic rock community dominated by passive suspension feeders with the grazing species *Echinus esculentus* and a scavenger/predator *Maja squinado.* Gannets Rock, Lundy. Image: Keith Hiscock.

Overhanging subtidal aphotic rock community dominated by opportunistic carnivores with the grazing species *Echinus esculentus*, the deposit feeder *Holothuria forskali* and active suspension feeders. Knoll Pins, Lundy. Image: Keith Hiscock.

Key: Very High ✓✓✓✓, High ✓✓✓ , Low ✓✓, Very Low ✓ Not Relevant NR, Not possible to manage NP

	Importance to biological community	Likelihood of change	Management priority
Physical & chemical properties & processes			
Wave action	✓✓✓	NP	NP
Tidal flow strength	✓✓✓✓	NP	NP
Immersion / emersion	NR	NP	NP
Salinity	✓✓✓	NP	NP
Supply of nutrients	✓✓	✓	✓
Supply of oxygen (availability in the water column)	✓✓✓	NP	NP
Availability of suitable substrata	✓✓✓✓	✓✓	✓✓
Light	✓	✓	✓
Contaminants	✓✓	✓✓	✓✓
Sedimentation	✓✓✓	✓✓	✓✓
Structure			
Physical (rock hardness, degree of slope, presence of other sediment)	✓✓✓	✓	✓
Biological (refuge, attachment surfaces, places to nestle and lay eggs)	✓✓✓	✓✓	✓✓
Biological - the presence / absence of particular species	✓✓✓✓	✓✓	✓✓
Functioning (as processes)			
Food supply remote (suspension feeding)	✓✓✓✓	✓✓	✓
Food supply local (grazing, predation)	✓✓✓✓	✓✓	✓
Primary productivity	✓✓✓✓	✓	✓
Connectivity (larval dispersal & recruitment)	✓✓✓	✓	✓

- There may be large differences in communities on vertical as opposed to gently sloping rock faces. There are several reasons for this including differences in levels of sedimentation, predator mobility and the availability of different habitats such as boulders and cobbles.
- Despite the apparent lack of light there may be some red algal species, especially encrusting coralline algae, towards the upper reaches of the habitat. Encrusting coralline algae are tolerant of intense sea urchin grazing.
- Although the absence of light prevents high amounts of primary productivity in this habitat, primary production is still vitally important since it brings organic carbon to the habitat in the form of phytoplankton, detritus and propagules which can be eaten by suspension feeders, detritivores and grazers etc.
- Many animals require localized food sources (obtained by grazing and predation) although barnacles and other suspension feeders feed from the water column. Vertical rocky communities may be dominated by suspension feeders since mobile predators may be restricted in terms of movement on vertical surfaces and particulate organic material, apart from where it gets trapped by various species and depending on water currents, is less likely to settle on the vertical surfaces to the detriment of grazers and detritivores.
- The animals associated with aphotic rocky communities are likely to be highly diverse and will include suspension feeders such sea fans, sponges, soft corals and anemones and predators including starfish and demersal fish.

Structure & functioning – characterization and importance for management habitat: Horse mussel (*Modiolus modiolus*) beds

Horse mussel bed in Shetland illustrating rich associated fauna. Image: Anon / Joint Nature Conservation Committee.

Fragmented group of horse mussels in sediment. Loch Duich. Image: Keith Hiscock.

Key: Very High ✓✓✓✓, High ✓✓✓ , Low ✓✓, Very Low ✓Not Relevant NR, Not possible to manage NP

	Importance to biological community	Likelihood of change	Management priority
Physical & chemical properties & processes			
Wave action	✓✓	✓	NP
Tidal flow strength	✓✓✓✓	✓	NP
Immersion / emersion	NR	✓	NR
Salinity	✓✓✓✓	✓	NP
Supply of nutrients	✓✓✓	✓✓	✓
Supply of oxygen	✓✓✓	✓✓✓	✓✓✓
Availability of suitable substratum	✓✓✓✓	✓✓✓✓	✓✓✓✓
Light	✓✓	✓	✓
Contaminants	✓✓	✓✓	✓
Sedimentation	✓✓	✓✓✓	✓✓✓
Structure			
Physical (structural heterogeneity – hard and soft substrata, stability from matrix)	✓✓✓✓	✓✓✓✓	✓✓✓✓
Biological (refuge, attachment surfaces)	✓✓✓✓	✓✓✓✓	✓✓✓✓
Biological - the presence / absence of particular species (namely *Modiolus modiolus*)	✓✓✓✓	✓✓✓✓	✓✓✓✓
Functioning (as processes)			
Food supply remote (suspension feeding)	✓✓✓✓	✓	✓
Food supply local (grazing, predation)	✓✓✓	✓	✓
Primary productivity	✓✓	✓✓	✓✓
Connectivity (larval dispersal & recruitment)	✓✓✓	✓	✓

- Horse mussel beds and their associated communities are dominated by the physical structure provided by the horse mussels themselves. The mussel matrix binds together the sediment and, depending on water flow, may lead to a build up of faecal mud and shell debris within the matrix, which supports a rich community of infauna.
- As a result of the complexity of the structure provided by these biogenic reefs, there exists a highly diverse habitat offering animals numerous different niches to occupy. As a result, horse mussel beds are extremely species rich habitats and support several commercially viable species, most notably scallops.
- Due to the depth at which these reefs often occur, water flow rate is the primary physical process responsible for bringing suspended food to the community. This process is essential because the community is dominated by suspension feeders that rely on suspended particulate organic material for nutrition.
- Horse mussel beds are found on both hard and soft substrata. On sediment, the mussels may be partly buried within the sediment whereas on rock, they are attached by byssus threads.

By far the greatest likely source of change to horse mussel beds is the physical disturbance of the habitat, the integrity of which, as explained above, is required to sustain the highly biodiverse community associated with the reefs. The most damaging physical disturbance to horse mussel beds recorded to date is scallop dredging which has led to the almost total destruction of horse mussel beds in Strangford Lough.

Structure & functioning – characterization and importance for management habitat: Transitional waters / estuaries

The River Yealm is a ria (a flooded river valley) that becomes increasingly less saline inland. Image: Keith Hiscock.

Transitional waters are often subject to input of waste and contaminants. Effluent from fish processing plant, Plymouth, 1986. Image: Keith Hiscock.

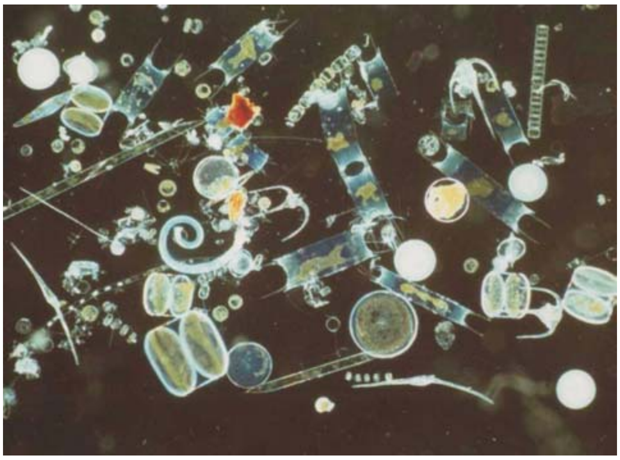
Key: Very High ✓✓✓✓, High ✓✓✓ , Low ✓✓, Very Low ✓ Not Relevant NR, Not possible to manage NP

	Importance to biological community	Likelihood of change	Management priority
Physical & chemical properties & processes			
Wave action	✓✓✓	✓	NP
Tidal flow strength	✓✓✓✓	✓	NP
Immersion / emersion	✓✓	✓	NP
Salinity	✓✓✓✓	✓	NP
Supply of nutrients	✓✓✓✓	✓✓✓	✓✓✓
Supply of oxygen (availability in the water column)	✓✓✓✓	✓✓✓	✓✓✓
Availability of suitable substrata	NR	✓✓	✓
Light	✓✓✓✓	✓✓	
Contaminants	✓✓✓✓	✓✓✓✓	✓✓✓✓
Sedimentation	✓✓✓	✓	✓
Structure			
Physical (stratification, suspended sediment levels)	✓✓✓	✓✓	✓
Biological (composition of plankton / predator community etc)	✓✓✓✓	✓✓✓	✓✓✓
Biological - the presence / absence of particular species	✓✓✓✓	✓✓✓	✓✓✓
Functioning (as processes)			
Food supply remote	✓✓✓✓	✓✓	✓✓
Food supply local (grazing, predation)	✓✓✓✓	✓✓	✓✓
Primary productivity	✓✓✓✓	✓✓	✓✓
Connectivity (larval dispersal & recruitment)	✓✓✓✓	✓✓	✓✓

- Transitional waters represent a highly variable physical and chemical habitat both temporally and spatially. This variability makes transitional waters a tough place to live and only some species are capable of withstanding it. In addition to the constantly changing physical and chemical environment, plants and animals must often contend with high levels of turbidity and suspended sediment, thermal and saline stratification of the water column, eutrophication and chemical contamination. Planktonic diversity decrease with distance from the sea.
- A characteristic of many estuaries is the 'turbidity maximum' – an area with higher suspended sediment than further up or down steam. This is generally at the limit of the saltwater intrusion. The high levels of suspended sediment are bad for suspension feeders (because they clog feeding apparatus) and for primary production, since light penetration is reduced.
- Consented sewage discharges (commonplace in many estuaries) have the potential to cause large changes in the levels of ammonia, pH and suspended material in the water column. Combined with riverine inputs, the nutrient levels in transitional waters are generally higher than in the open ocean.
- Tidal flow and wind stress both contribute to mixing transitional waters that may otherwise be stratified. The main reason underpinning stratification of the water column in transitional waters is the difference in density between fresh water and sea water. Where rivers flow into estuaries, the lower density fresh water lies on top of heavier seawater as a separate layer. Mixing is important for allowing oxygen penetration into the lower layers and to prevent sharp gradients of, for example, temperature and nutrient availability that may would otherwise be detrimental to certain plants and animals.
- In some transitional waters, such as in fjordic systems, there is little mixing of the bottom layers and, as a result, the bottom layers may become anoxic.
- The only primary producers in the water column are the phytoplankton although allochthonous sources of primary production will come from microphytobenthos and macroalgal detritus.
- In addition to particulate organic matter, dissolved organic matter and its breakdown by microbes is also an essential element of pelagic food webs in transitional waters.

The most likely change in the character of transitional waters will be as a result of chemical factors, such as eutrophication (excess nutrient loading), oil pollution or synthetic chemical contamination. Sewage effluent has a high Biological Oxygen Demand (BOD), meaning that the work involved breaking down all the organic material within it is such that the organisms responsible would use high amounts of oxygen in the process. As a result, there would be less oxygen available in the water column. Furthermore, metals such as mercury, cadmium and lead can be found within the effluent.

Structure & functioning – characterization and importance for management habitat: Offshore pelagic (stratified) areas


Phytoplankton biomass is driven by light, nutrients and the seasonal occurrence of species. Image: Norman Nicoll / www.naturalvisions.co.uk


Ultimately, the food chain leads to top predators such as dolphins. Image: Judith Oakley.

Key: Very High ✓✓✓✓, High ✓✓✓ , Low ✓✓, Very Low ✓Not Relevant NR, Not possible to manage NP

	Importance to biological community	Likelihood of change	Management priority
Physical & chemical properties & processes			
Wave action	✓✓✓✓	✓	NP
Tidal flow strength	✓✓	✓	NP
Immersion / emersion	NR	NR	NR
Salinity	✓✓	✓	NP
Nutrients	✓✓✓✓	✓✓	NP
Supply of oxygen	✓✓✓✓	✓✓	✓
Availability of suitable substrata	NR	NR	NP
Light	✓✓✓✓	✓	NP
Contaminants	✓✓✓	✓✓✓	✓✓✓
Sedimentation	✓✓	✓	✓
Structure			
Physical (stratification)	✓✓✓✓	✓✓	NP
Biological – plankton (composition including addition of non-natives)	✓✓✓✓	✓✓✓✓	✓✓✓✓
Biological – predators (composition including addition of non-natives)	✓✓✓✓	✓✓✓✓	✓✓✓✓
Functioning (as processes)			
Food supply remote (suspension feeding)	✓✓	✓✓	NP
Food capture - local (predators)	✓✓✓✓	✓✓✓✓	✓✓✓✓
Primary productivity	✓✓✓✓	✓✓✓✓	NP
Connectivity (larval dispersal & recruitment)	✓✓✓✓	✓	✓

- Turbulence determines the depth to which water is ‘agitated’ and a thermocline is therefore unlikely to form. The wave base is likely to be about 100 m in offshore areas. During calm weather, surface water heats-up and a discontinuity between warm and cold water develops.
- The strength of the thermocline, and therefore the degree of turbulence needed to break it, is important and will be determined in part by the amount to which shallow waters are heated.
- The layer thermocline is predominantly important in causing stratified waters and the stratification is a barrier to nutrients being transported from deeper waters to the surface.
- Tidal flow can contribute to the thermocline breaking-up.
- Salinity can be important to the development of a pycnocline which may be co-incidental with the thermocline.
- Tropic mismatches may occur as preferred plankton food of fish larvae may become out of synchrony with each other – most likely as a result of warming seas.
- Predators (fish, sharks, cetaceans) are exploited directly or may be by-catch. Over-exploitation may result in a switch to jellyfish dominated communities and therefore less possibility of recovery.
- Pelagic offshore systems are open systems where human activities are unlikely to affect connectivity between areas.
- Non-native species may have a harmful effect on plankton and on larger predators especially where the non-native species poison (for instance dinoflagellate algae) or consume (for instance jellyfish consuming zooplankton including larval fish).

As stratification becomes increasing strong as a result of seawater warming (which is predominantly of shallow waters), there is a danger that nutrient transfer from deeper to shallower waters is blocked and shallow productivity declines.

Many potential changes are indicated as “Not possible” to influence. These changes are being driven by global climate change which requires global management actions.

Research Information Note

English Nature Research Reports, No. 699

The structure and functioning of marine ecosystems: an environmental protection and management perspective

Hiscock, K., Marshall, C., Sewell, J. & Hawkins, S.J., 2006.

Keywords: ecosystem, structure, function, processes, marine

Introduction

Ensuring that the seas around the UK are "*clean, healthy, safe, productive and biologically diverse*" (Defra, 2002) whilst continuing to provide the goods and services that society uses requires:

- knowledge and understanding of what is where and how it varies with time, including physical, chemical and biological **properties**;
- knowledge and understanding of the **processes** that influence properties at a location, and
- management that understands:
  - the role of **structural features**;
  - the interaction of physical, chemical and biotic **processes** that shape ecosystem **functioning**, and
  - the importance of biological diversity in the above.

What was done

The Marine Biological Association were commissioned as a result of an open tender process to provide a report setting out, in an easy to read and well illustrated format, an environmental management and protection perspective to the structure and functioning of marine ecosystems

Results and conclusions

This report accordingly provides:

- a summary of marine ecosystem goods and services;

Continued……

- a description of major large-scale properties and processes;
- an account of ecosystem structure and functioning in the marine environment and examples of how environmental change from human activities may affect ecosystem structure and functioning;
- the role of resilience, resistance and recovery in maintaining the baseline conditions;
- examples of how the limits of ecosystem resilience and resistance may be reached, and
- dossiers of critical ecosystem structure and functional processes within particular environments (marine landscapes).

The information listed above will support the 'Ecosystem Approach' to marine environmental management, protection and education. The case studies given in the report are only examples but can be used to inform the importance of different aspects of properties, structure and functioning (as processes) for management of areas to maintain ecosystems and the services they provide.

English Nature's viewpoint

Sustainable development is dependent on a continued flow of benefits from the marine environment, both in terms of direct relationships, such as providing a source of food, but also in relation to more (perceived) indirect benefits, such a climate regulation. This report is a significant contribution towards drawing out the existing science so a wider audience better understanding these processes and what it really means to apply the Ecosystem Approach.

Selected references

DEFRA. 2002. *Safeguarding our seas. A strategy for the conservation and sustainable development of our marine environment*. Defra: London.

HISCOCK, K., MARSHALL, C., SEWELL, J., & HAWKINS, S.J. 2006. *The structure and functioning of marine ecosystems: an environmental protection and management perspective*. Report to English Nature from the Marine Biological Association. Plymouth: Marine Biological Association.

Further information

English Nature Research Reports and their *Research Information Notes* are available to download from our website: www.english-nature.org.uk

For a printed copy of the full report, or for information on other publications on this subject, please contact the Enquiry Service on 01733 455100/101/102 or e-mail enquiries@english-nature.org.uk

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Front cover photographs:
Top left: Using a home-made moth trap.
Peter Wakely/English Nature 17,396
Middle left: Co_2 experiment at Roudsea Wood and Mosses NNR, Lancashire.
Peter Wakely/English Nature 21,792
Bottom left: Radio tracking a hare on Pawlett Hams, Somerset.
Paul Glendell/English Nature 23,020
Main: Identifying moths caught in a moth trap at Ham Wall NNR, Somerset.
Paul Glendell/English Nature 24,888